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Skusella Freeman (Diptera: Chironomidae): new species, immature stages from Africa, Asia and Australia, and expanded distributions

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Abstract

Skusella Freeman, 1961 (Diptera: Chironomidae, Chironominae), known previously from adults from Australia and Africa, is revised with extended descriptions, including for immature life stages. *Skusella* is diagnosed based on its type species *S. subvittata* (Skuse, 1889) from Australia, *S. pallidipes* (Kieffer, 1921) from the Afrotropical region (the only other originally included species), a second African species *S. freemani* Harrison, 2002, and *S. silingae* Tang, **sp. n.**, newly described here from the pupa and adult males from China. The immature stages of *Skusella* have been known informally for several decades, notably for a characteristic fringe of setae on one or more abdominal pleurae of the pupa, shared only with newly described Paraskusella Cranston, 2018 within the Chironominae. Amongst larvae of Chironomini with 6-segmented antenna, alternate Lauterborn organs and a well-demarcated ventromentum, those of *Skusella* are distinguishable only with caution due to insufficient reared associations. Unassociated pupal exuviae, tentatively belonging to three unknown new species, are described informally from China, as is a larval type from Africa. Range extensions include for *S. freemani*, with pupae (newly described here) from Nigeria and Cameroon, at least 5000 km from the type locality in South Africa. A wider distribution of *S. subvittata* in Australia and Asia is revealed by extensive pupal exuviae sampled from drift.

Key words: new species, pupal fringe, range extension, immature stages

Introduction

In his revision of the Australian Chironomidae, Freeman (1961) used a narrower generic concept than in prior papers on the African Chironomidae (*e.g.* Freeman 1957, 1958). For example, species assigned to the northern hemisphere-based "*Chironomus (Endochironomus)* Kieffer" (Freeman 1957) or "*Lauterborniella* Thienemann & Bause" (Freeman 1958) thereafter were transferred to *Conochironomus* Freeman or *Skusella* Freeman as new Afro-Australian taxa (Freeman 1961). Although based originally only on adults, these more restricted groups have found support from phylogenetic analyses of morphology of all life stages and from molecular data (*e.g.* Cranston *et al*. 2011). *Conochironomus*, revised on morphology by Cranston & Hare (1995), in addition to its Afro-Australian range now has Asian endemic species (Cranston 2016). Likewise *Skusella*, believed also to be restricted to Africa and Australia by Freeman (1961), was reported in a guide to the larval chironomids of south-east Asia (Cranston 2004) that lacked further data. More recently pupal exuviae and adults of *Skusella* have been found in southern (Oriental) China by the present junior author. It is appropriate now to enhance the adult diagnosis, provide the first formal generic diagnoses for larvae and pupae, describe a new species and document a wider distribution for *Skusella*. We describe and illustrate taxa with what we consider a diagnostic setal fringe on one or more pupal abdominal pleurae. Keys, redescriptions, and descriptions of new species and immature stages presented will allow species or morphotype recognition. This should encourage incorporation of these insects in aquatic environmental

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monitoring programs, increase understanding of freshwater insect biodiversity, and perhaps inspire more rearing of regional chironomids for which full associations are lacking (Cox *et al*. 2007).

Methods

Collecting included kick netting and disturbance of lotic and lentic marginal habitats for larvae and pupae. Pupae, exuviae and drowned pharate adults were sought also by exposing drift nets with a 300 µm mesh to intersect flowing water surfaces. Adults were sought by sweeping marginal vegetation and some light trapping beside water. Collections usually were field-sorted with a dissector microscope. Individual rearing met with minimal success and life history associations from intercept of drift were very rare. Mass rearing from bulk sediments by the junior author met with higher success, although larval exuviae were not recovered. No molecular material other than that mentioned in Cranston *et al.* (2011) has been studied.

Most specimens were prepared as slides mounted in Euparal using standard procedures (Cranston 2000), but some loaned specimens had been slide mounted without prior clearing by the late F. Reiss (ZSM), and Landis Hare's mounts from Nigeria are in Canada Balsam. Identifications of larvae, pupae and adults were made using a compound microscope with phase contrast and Nomarski optics, and a wide range of identification tools. Australian material examined is listed clockwise by state from Northern Territory to Western Australia. Information additional to label data is placed in square parentheses [ ]. The same square brackets are used for other authors' mensural data in our redescriptions.

Morphology. Morphological terminology follows Sæther (1980), Cranston (1995, 2013) and Cranston *et al*. (1989), as applicable. Interpretation of the median volsella follows Pinho *et al*. (2013) in that this appendage originates in a plane between the superior and inferior volsella. Morphological measurements, unless otherwise stated, are in µm rounded to the nearest 5 µm except when measurement at maximum magnification (oil immersion, x1000) provided accuracy to +/- 1 µm. In keeping with our understanding of the influence of body size variation = allometry, see McKie & Cranston (2005), here we provide only the summaries of antennal flagellomere and leg segment ratios but not the actual measurements (which can be obtained from the authors on application).

Images. Photographs were taken with a Leica™ DMRX compound microscope with either phase or Nomarski™ interference optics, with images manipulated with Automontage™ to allow automated retention of focused parts of exposures at different depths. Post image-capture manipulations were made in Adobe® Photoshop™. Ink drawings were made by hand using a drawing tube, or from photographic images scanned for editing. In line drawings of the complete pupal abdomen (Figs 5, 6) the posterolateral 'comb' (Fig. 4H–J) is portrayed as if on the same dorsal plane as the tergal structures, although the comb actually lies more on the ventral surface (pleural / sternal). This follows existing convention (*e.g.* Pinder & Reiss 1986) as does some imprecision about the plane of origin of lateral abdominal setae.

Mapping. The distribution map (Fig. 9) was made using ArcGis™ software, with all possible GPS locations of 11 taxa implanted into the vector of World Map (http://www.vectorworldmap.com). For older specimens without precise location details, estimates were made from the finest available detail (*e.g.* city / country) available from either specimens or publications.

Abbreviations. *ACT*, Australian Capital Territory (Australia); *Ant* (1–6), antennal segment lengths (larva); *AR*, Antennal Ratio = (adults): length of terminal flagellomere divided by combined length of preceding flagellomeres), (larva): length of basal segment divided by combined lengths of segments 2–6; *B.l.,* Body length (an approximation) in mm; *BV*, "Beinverhältnis": length of femur, tibia plus first tarsomere / combined length of tarsomeres 2–5; *Clyp*, clypeus setae (count); *Ck*, Creek; *Dc*, dorsocentral setae (count); *E*, East; *Gcx*, gonocoxite length; Fl_{1-12}, antennal flagellomere lengths 1–12 combined (adult male); *Gst*, gonostylus length; *H.l*., head capsule length (larva); *L*, larva; *L.aps,* lateral antepronotals; *Le*, larval exuviae; *Le/Pe/*♂*(*♀*)*, reared adult male (female) with associated larval skin, pupal exuviae; LR_n, Leg Ratio = tarsomere 1 length / tibia length; *MV*, molecular voucher; *Mvo*, median volsella; *n*, number of specimens measured; *N*, North; *NNR*, National Nature Reserve; *N.P.*, National Park; *NSW*, New South Wales (Australia); *NT*, Northern Territory (Australia); P_{1-3}, Leg(s) (1 = fore, 2 = mid, 3 = hind leg); *Pa*, prealar setae (count); *Palp*, palpomere lengths; *P(e),* Pupa (exuviae); *Prov.*, province (Thailand); *Qld*, Queensland (Australia); *R*., River; *R,* $R_{1,}$ $R_{2+3,}$ R_{4+5}, respective setae (count) on wing veins R, $R_{1,}$ $R_{2+3,}$ R_{4+5}; *S*, South; *SA*, South Australia; *Scts*, scutellar setae (count); *SV*, "Schenkel-Schiene-Verhältnis" =

combined length of femur and tibia / length of first tarsal segment; *Svo*, superior volsella; *TIX*, male tergite IX setae (count); *Vic*, Victoria (Australia); *VmPR*, ratio of ventromental plate length / width; *V.R.*, vein ratio = length of Cu / length of M; *W*, West; *WA*, Western Australia; *Wl*, Wing length (arculus to apex) in mm.

Institutions: ANIC, Australian National Insect Collection, CSIRO, Canberra, Australia; EJNU, Institute of Groundwater and Earth Science, Jinan University, China; NHM, The Natural History Museum, London, UK; TMSI, Tropical Marine Science Institute, National University of Singapore; WAM, Western Australian Museum, Perth, Australia; ZSM, Zoologische Staatssammlung München, Munich, Germany.

Taxonomy

Skusella Freeman

(Figs 1–8)

Skusella Freeman, 1961: 718.
Skusella Freeman; Cranston (1996): L, P; Cranston (2004): L; Harrison (2002): M, F.

Type species: *Chironomus subvittatus* Skuse, 1889: 246, by original designation.
Other included species: *Skusella pallidipes* (Kieffer, 1921), Africa; *Skusella freemani* Harrison, 2002, Africa; *Skusella silingae* Tang **sp. n.,** Asia.

Generic diagnosis

Male. Small to medium-sized, with body length 2.7–6.8 mm, wing length 1.3–2.7 mm. Wing hyaline, plain (Fig. 1A) or dark patterned (Fig. 1B). Thorax yellow-brown with darker postnotum, legs plain or with darkened 'knees' (femoral apices, tibial bases) on pale legs.

Antenna. With 13 flagellomeres. Antennal ratio 1.1–1.6.

Head. Eye bare, with strong, parallel-sided dorsomedial extension 8–10 ommatidia long; in male separated medially by about width of 4 ommatidia, eyes of female almost contiguous. Uniserial temporal setae comprise outer verticals and postorbitals; clypeals present. Frontal tubercles absent. Palp 5-segmented, segment 2 globular, segments 3 to 5 increasingly elongate; segment 3 apparently lacking sensilla.

Thorax (Fig. 1C). Antepronotal lobes strongly tapered dorsally, medially almost divided, with 0–6 lateral antepronotal setae. Scutum not or at most slightly overreaching antepronotum, profile with one or two scutal humps of variable size along the longitudinal midline, or nearly smoothly curved. Acrostichals absent, dorsocentrals uniserial, prealars and scutellars few, uniserial.

Wing (Figs 1A, 1B). Membrane weakly punctate, without setae or microtrichia. Anal lobe weak. Costa ending abruptly at apex of R_{4+5}, which terminates in C just proximal to wing apex; R_{2+3} ending near proximal 1/4 between R_1 and R_{4+5}. FCu slightly distal to RM. Brachiolum with 2–3 setae. R setose, R_1 and R_{4+5} setose in some males only. Squama with 0–5 setae.

Leg. Apex of fore tibia with rounded to triangular scale, without spur (Fig. 1D). Mid and hind tibiae apically with two nearly contiguous combs, together occupying about half of tibial circumference; only inner comb with apically hooked spur, the other with scarcely indicated spur (Fig. 1E). Foreleg ratio 1.6–2.4. Midleg tarsomere 1 with few, uniserial sensilla chaetica in apical third, or sensilla apparently lacking. Pulvilli very small.

Abdomen. Tergites I–VII with few, irregularly scattered setae.

Hypopygium (Figs 1F, 1G, 2A, 2D). Anal tergite bands weak to strong, separated medially to form incomplete V-shape; median anal tergite setae sparse or absent; posterior margin of tergite IX with few to many setae near origin of anal point. Anal point nearly parallel-sided to spatulate apex rounded to bluntly tapering. Superior volsella (Figs 1H–I, 2B, 2E) more or less swollen basally, distally crescent-shaped, narrowing to rounded or pointed apex in same horizontal plane as base; volsella without microtrichia, with 2–4 medially directed setae near inner margin, and 0–2 outer setae. Median volsella (Figs 1J, 2C, 2F) total length 80–90 µm, with slender stem, distally with variably dense simple or narrowly taeniate setae. Inferior volsella appressed basally to gonocoxite, somewhat angled in dorso-ventral plane, distally short and broadly subglobular, extending no further than

gonocoxite apex; volsella microtrichiose apico-ventrally, apically with medially and dorso-medially directed, simple setae, without differentiated, posteriorly-directed strong seta. Gonostylus slender, straight to slightly inwardly curved, slightly tapering, apex rounded. Transverse sternapodeme shallow (Fig. 2A) to broadly plate-shaped, antero-lateral projections modest and bluntly rounded, or absent. Phallapodeme variably distinct.

Female. Body length 2.9–4.4 mm; wing length 1.5–2.6 mm.

Antenna with 5 flagellomeres, AR 0.41–0.44. Thorax as in male, except dorsal 'hump(s)' better developed. Wing as in male, except veins R, R, and R_{4+5} setose in all females examined.

Genitalia (Figs 3A–E). Notum long, thin, with fine rami of varying relative length. Gonocoxapodemes not fused medially, each gently curved, with apparent weak branch into gonapophysis VIII. Coxosternapodeme strongly sclerotized, sinuous. Gonapophysis VIII divided into elongate dorsomesal lobe, essentially continuous with inner contour of vagina, microtrichiose except hyaline apico-medially, and distinct ventrolateral lobe at least as large as dorsomesal lobe, lying lateral to, and not covering, dorsomesal lobe, microtrichiose basally, with pointed scales medio-apically. Apodeme lobe not evident. Labia well developed, without microtrichia. Gonocoxite IX small, not laterally extended, with 2–5 short lateral setae. Tergite IX broad, undivided. Postgenital plate microtrichiose and microsetose. Seminal capsule pale, oval to elongate-oval with variably distinct neck; spermathecal duct slightly (Fig. 3A) to strongly sinuous (Fig. 3D) or with complete loop (Fig. 3E), ending separately or in apparently common opening. Cerci small, quadrate.

Pupa. Medium-sized, 4.1–6.0 mm long. Thorax and cephalic area golden brown, abdomen pale with golden-brown apophyses, combs and anal lobes.

Cephalothorax. With or without cephalic tubercles; frontal apotome smooth or weakly wrinkled, without frontal warts; frontal setae absent or weak to strong (Fig. 4A). Thoracic horn very hyaline and difficult to see in detail in slide preparations, with 6 smooth branches subequal in length (Fig 4B); basal ring (Fig. 4C) small, oval, with 1 smaller, oval tracheal bundle. Median sutural area variably rugose with scales, or nearly smooth. Prealar tubercle triangular (Fig. 4D) to rounded, weak or absent. Antepronotum with 1 median, 0–2 lateral setae; 2 precorneals; dorsocentral seta (Dc) 1 close to Dc_2, the two far separated from the approximated Dc_3 and Dc_4, all subequal and c. 50–75 µm long.

Abdomen (Figs 4E–G, 5A–C, 6A–C, Tergite I unarmed or with anterior fine shagreen (Figs 5A, 5C) T II–VI with variably extensive, triangular to subquadrate medio-posterior area of spinules, paratergites armed or unarmed T VII–VIII with transverse antero-lateral spinule areas, except in *S. freemani* (Fig. 5C). T IX unarmed. Tergite II hook row continuous, short, comprising 20–31 hooks, covering c. 20–30% width of segment II. Conjunctives bare. Sternite and parasternites I bare or sometimes with anterior spinules (Fig. 4E); other sternites bare or with spinule pattern approximating that of corresponding tergite, and more extensive on S VIII. Vortex absent. Segment I with (Fig. 4E) or without antero-lateral tubercles; pedes spurii B weak to well developed only on segment II (*e.g.*, Fig. 4G). Posterolateral margin of sternite/parasternite VIII with transverse 'comb' of clustered small, golden-brown teeth, the latter either small, subequal and linearly arranged (Figs 4H, 8B) or more clumped and with teeth distinctly larger centrally than more laterally (Fig. 4I). Apophyses modestly developed. Segment I with 2D, 3V and without L setae; II with 3D, 3V and 3 L; III with 4D, 3V and 3L; V–VII with 5D, 3–5 V and 1 or 2 non-taeniate L, VIII with 1D, 2V, all strong, and without L setae. Pleurae of at least segment VIII with characteristic fringe of taeniate setae (Figs 4G, 5A–C, 6A–C). One pair of O setae on segments II–VII. Anal lobe (Fig. 8A) somewhat elongate to semicircular with c. 100–140 multiserial taeniate setae in fringe, denser apically, reaching apex of lobe; anal lobe with 1 taeniate dorsal seta. Genital sac of male reaching slightly beyond anal lobe, sac of female significantly shorter.

Larva (4th instar). Medium-sized, body length c. 8–10 mm but rarely measurable in present material, ventral head length (= postmentum length sensu Sæther 1980) 195–235 µm. Body colour pink-red; head capsule pale yellow except for golden dorsomental, apical mandibular and premandibular teeth; narrow occipital margin scarcely darker than genae and submentum.

Dorsal surface of head (Figs 7A) with frontoclypeus lacking a fenestra: demarcation of labral sclerites recognisable only by granulosity.

Antenna (Figs 7B–C, 8D) appearing 7-segmented due to segment 2 being subdivided by unsclerotized section near mid-length and Lauterborn organs on apices of apparent 3rd and 4th segments. Segment 1 with ring organ in basal third, seta absent. Blade extending to near apex of third antennal segment.

Labro-epipharyngeal region (Figs 7D, 8F). SI and SII plumose with about 25 apical branches; SIII simple,

short; SIVa and b moderately developed. 6–7 plumose chaetae. Seta praemandibularis simple. Lamellae broad, with weak indication of median division. Pecten epipharyngis of three scales, each apically with 4–6 uneven-lengthed teeth in flat plane. 7–8 deeply plumose chaetulae laterales, 2 apically branched chaetulae basales. Premandible with 3 teeth and very strong brush (Fig. 7E, 8F).

Mandible (Figs 7F, 8C, 8E). Strong dorsal tooth present, slightly paler than remaining teeth; strong apical tooth and 2 inner teeth. Pecten mandibularis well developed, not extending beyond dorsal or apical tooth. Seta subdentalis arising from ventral surface, long and sickle-shaped. Mola and inner margin smooth. Seta interna consisting of several plumose branches.

Mentum (Figs 7G–H, 8C) with 16 uneven-sized teeth, the fifth teeth from the side projecting farthest forward; clearly demarcated antero-medial section (ventromental component) comprising four (Fig. 7G) subequal, paler teeth, lateral dorsomental components with six darker teeth decreasing in size laterad.

Ventromental plates separated medially by the median ventromental mental teeth; plate fan-shaped, with curved, smooth anterior margin, except for variably indicated anteromedial hump(s); without striae visible in middle or posterior of plate, but with an outer submarginal row of lappets, apparently lacking hooks. Setae submenti simple.

Abdomen. Anterior parapod claws dense, fine, simple; posterior parapod claws simple. Posterior segments without lateral or ventral tubules. Procercus unpigmented, small, as high as wide, bearing 4–5 anal setae.

Comments. Adults of *Skusella* were distinguished by Freeman (1961) on morphology, especially the leg spurs, namely fore tibia with plain, oval scale, combs of mid and hind tibiae nearly fused, with one long apically hooked spur. Although the curvature of the spur varies, perhaps by orientation, this allows separation from *Conochironomus* with conical combs, and from otherwise similar genera. The absence of acrostichal setae in *Conochironomus* and *Skusella* distinguishes from *Paratendipes*, in which these setae are strong. The smooth (non-creased) dorsomedian surfaces of the gonostylus in *Skusella* distinguish from *Conochironomus* as does the median volsella, present only in *C. avicula* Freeman, 1955 and *C. deeming* Cranston & Hare, 1995. The female genitalia in *Skusella* show a shallowly curved gonocoxapodeme (straight in *Conochironomus*, deeply rounded in *Paratendipes*) and, in contrast to the single gonapophysis VIII lobe in *Paratendipes*, two lobes are present in *Skusella* and *Conochironomus*. These features may not hold up against wider sampling of more associated females. Molecular analysis shows *Conochironomus* and *Skusella* as sister taxa (Cranston *et al*. 2011) and thus morphological similarity is to be expected, but *Paratendipes* and other likely relatives were lacking in that study and differentiation is not conclusive. See below for further discussion concerning generic delimitation.

Pupae of *Skusella* are recognised by the lateral fringe of taeniate setae on at least pleura VIII. Which is unique in the subfamily Chironominae (see further discussion under pupae below).

Among genera with larvae bearing alternate Lauterborn organs on a six-segmented antenna, *Skusella* resembles *Conochironomus* and *Paratendipes* (Cranston 2016). The location of the basal Lauterborn organ in *Skusella* on the apparent 3rd segment distinguishes from *Conochironomus*, in which it is located at the apex of the 2nd segment as in most taxa with alternate Lauterborn organs. However, at least one undescribed N. American and one Australian *Paratendipes* larva have the basal Lauterborn organ arising in the middle of the second antennal segment. All *Conochironomus* larvae that have been associated with other life stages have the 3rd antennal segment narrowed basally alongside the basal Lauterborn organ, and dilate apically, whereas in *Skusella* the (apparent) 3rd antennal segment is parallel-sided. The pecten epipharyngis has distinctly toothed scales in *Skusella* and *Conochironomus*, but in *Paratendipes* these scales usually are simple although serrate in some taxa (Epler *et al*. 2013, repeated from Pinder & Reiss 1983). In contrast to the four protruding median mental teeth in *Conochironomus,* the 'ventromentum' in *Skusella*, *Paratendipes* and the related taxa under discussion comprises more than four teeth that are either subequal in size to the laterals, or smaller than at least one prominent lateral tooth.

Key to species and known life stages of adult male *Skusella* Freeman

1 Wing patterned (Fig. 1B) 2
Wing unmarked (Fig. 1A) 3
2 Legs uniformly pale. Squama bare . . . . . *S. pallidipes* Freeman
- Distal femur + proximal tibia dark. Squama setose . . . . . *S. freemani* Harrison
3 Anal tergite median seta absent. Superior volsella with 2–3 lateral setae, outer seta absent (Fig. 1H–I), anal point parallel-

sided, with bluntly tapered apex (Fig. 1F) . . . . . *S. subvittata* (Skuse)
- Anal tergite with 2–4 median setae. Superior volsella with 3–4 lateral setae, outer seta present (Fig. 2E), anal point somewhat spatulate distally, with rounded apex (Fig. 2D) . . . . . *S. silingae* **sp. n.**

Key to species and known life stages of adult female *Skusella* Freeman

1 Wing unpatterned (Fig. 1A). Seminal ducts gently curved (Fig. 3A) to near straight. Australia / Asia . . . . *S. subvittata* (Skuse)
- Wing patterned (Fig. 1B). Seminal ducts sinuous (Fig. 3D) or looped (Fig. 3E). Afrotropical 2
2 Legs pale. Squama bare. Seminal ducts sinuous (Fig. 3D) . . . . . *S. pallidipes* Freeman
Distal femur + proximal tibia dark. Squama setose. Seminal ducts with loop (Fig. 3E) . . . . . *S. freemani* Harrison

Key to species and known life stages of pupal *Skusella* Freeman

1 Pleural fringe on posterior of III and all of IV–VIII (Figs 5A, 5C, 6A–C). 2
- Pleural fringe restricted to VIII (Fig. 5B) 6
2 Spinulation on T II–IV barely extending to the lateral longitudinal row of muscle marks anteriorly; thus, spinule field narrower anteriorly than posteriorly (Figs 5A, 5C, 6A) 3
- Spinulation on T II–IV extending beyond lateral longitudinal row of muscle marks anteriorly; thus field wider anteriorly than posteriorly (Figs 6B–C). 5
3 With 25 or more hooklets on T II, occupying > ¼ of segment width (Fig. 6A) . . . . . *S. silingae* Tang **sp. n.**
- With 20 or fewer hooklets on T II, occupying about 1/5 of segment width (Fig. 5A) 4
4 Tergites VII and VIII spinulose (Fig. 5A). . . . . *S. subvittata* (Skuse)
- Tergites VII and VIII bare (without spinules) (Fig. 5C) . . . . . *S. freemani* Harrison
5 Pleurae II–IV bare, spinulose only on anterolateral of pleurae V–VII (Fig. 6B). Sternite I bare . . . . . *S.* sp. 'Limuling'
- At least pleurae II–IV spinulose (Fig. 6C). Sternite I with anterolateral and median spinule patches (Fig. 4E)*S.* sp. 'Sanyatang'
6 Tergites II–VI spinulation extending to apophyses on III–VII (Fig. 4F) . . . . . *S.* sp. 'Jianfengling'
- Tergites II–VI with spinulation not reaching apophyses (Fig. 5B) . . . . . *S. pallidipes* Freeman

Descriptions

Skusella subvittata (Skuse)

(Figs 1A, C, E, F, H; 3A–C; 4C–D, G–H; 5A; 7A–B, D–G; 8A–F)

Chironomus subvittatus Skuse, 1889: 246; Kieffer (1906: 22; 1917: 208).
Skusella subvittata (Skuse); Freeman (1961: 718); Cranston (1996: 48).

Material examined. Holotype. ♂ slide mounted in Euparal by Cranston: 'Walcha' [AUSTRALIA, New South Wales], '*Ch. subvittatus* ♂ type', F.A.A. Skuse, ANIC [no collection date].

Other material (collected Cranston, deposited ANIC, unless otherwise stated). AUSTRALIA: Northern Territory, 5Pe, nr. Narbaluk, Cooper Ck, 12°18'S 133°20'E, 27.v.1988; 1L, U. Magela Ck, Stoned Billabong, 12°38'S 132°53'E, 14.iv.1989; 1P♂, U. Magela Ck, below Bowerbird Billabong, 12°47'S 133°03'E, 28.v.1988; 2L, Upper Magela Ck, above falls, 12°47'S 133°36E, 15.iv.1989; 1L, 2Pe. 1Le/Pe/♀, Wildman R. at Arnhem Highway Crossing, 12°50'S 132°01'E, 2.vi.1988; 2Pe, Hickey Ck, 12°55'S 132°50'S, 29.v.1988; 2Pe, S. Alligator R. at Kakadu Highway ford, 13°17'S 132°19'E, 26.v.1988; 1Pe, Jim Jim Ck, above falls, 13°17'S 132°51'E, 29.v.1988 (*Dostine*) (ARRRI); 1Pe, Jim Jim Gorge, 21.xi.1989 (*Dostine*) (ARRRI); 1Pe, Graveside Gorge, 13°18'S 132°32'E, 17.vii.1988 (*Dostine*) (ARRRI #165); 1Pe, Koolpin Gorge, 13°30'S 132°35'E, 15–16.v.1992; 1♂, Kambolgie Ck, 13°32'S 132°23'E, 25.v.1988; 1Pe, S. Alligator R. at Fisher Ck., 13°33'S 132°33'E, 24.v.1988; 1Le/P, 1Pe, Gimbat, 13°34'S 132°35'E, 24.v.1988; 2♂, Coronation Hill, 13°35'S 132°36'E, 4/5.vi.1988; 3Pe, [Nitmiluk N.P.] Katherine R., below gorge 1, 14°20'S 132°25'E, 21–22.v.1992; 1♂, Caranbirini W.H., 33 km s.w. of Borroloola, 16°19'S 136°05'E, 3.xi.1975 (*Upton*, Macarthur R. survey), 1♂, 36 km s.w. of Borroloola, 4.xi.1975; 14 km s.w. Cape Crawford, 16°47'S 135°45'E, 25.x.1975.

Queensland, 1♂, 18 km w. Mt. Carbine, McLeod R., 16°49'S 145°00'E, 7.i.1982 (*Baehr*) (ZSM); 1♂, 2 km e. Einasleigh, Einasleigh R., 18°34'S 144°06'E, 11–12.vi.1993 (*Baehr*) (ZSM); 1P/♂, Lawn Hill N.P., Musselbrook Ck., upper pool, 18°37'S 138°08'E, 8.v.1995; 1♂, Louie Ck., Lawn Hill Crossing, 18°45.39'S 138°31.15'E, 17.v.1995, swept; 1♂, same except light trap.

New South Wales, 1L, nr. Wooli, Lake Hiawatha, 2 m. benthic, 29°48'S 153°09'E, 1.vii.1971 (*Timms*); 1L, Barrington Tops, Williams River at Rocky Crossing, 32°07'S 151°29'E, 8.xii.1993 (*Sydney Water*); 1L, Bardon, Dusodie, 'New Park', Chichester R., 32°26'S 151°69'E, 8.xii.1993 (*Sydney Water*); 4Pe, nr Araluen, Deua N.P., Deua R., 35°45'S 149°57'E, 29.iii.1989.

Victoria, 2Pe, Little Beetle Lake, 37°47'S 148°25'E, 17.xii.1996 (*Wright*).

Western Australia, 1P(♂), Pilbara, Fortescue R., Fortescue Falls, 22°29.00'S 118°33.06'E, CLM 26M (*Smith*); Hamersley Range N.P., Circular Pool, Fortescue Falls, 22°28'S 118°33'E, 23–24.iv.1992; 1Pe, Hamersley Gorge, 22°29.00'S 118°33.06'E, 22.iv.1992; 4Pe, Millstream Chichester N.P., Chinderwarrinder Pool, 21°35'24"S 117°04'02"E, 25.iv.1992; 1Pe, Crossing Pool, 21°34'22"S 117°05'02"E, 24.iv.1992; 1Pe, 7♂, Millstream Chichester N.P., Fortescue R., below Homestead, 21°33'S 117°03'E, 24–25.iv.1992; 1Pe, Willare Bridge, Fitzroy R., 17°44'08"S 123°38'45"E, 28.iv.1992; 1♂, 30 km s. Warmun, Frog Hollow Ck, 17°16'S 128°03'E, 14–15.1984 (*Baehr*) (ZSM); Pe, Manning Gorge, 16°39'S 125°56'E, 30.v.1992; 10Pe, Drysdale R. crossing, 15°41'S 126°47'E ,1–2.v.1992; 2Pe, King Edward R., 14°53'S 126°12'E , 5–6.v.1992; 1♂, 14 km s.e Kalumburu, CALM site #4/3, 14°25'S 126°40'E, 3–6.1988 (*Weir*); 2Pe, Old Boab Camp, Crystal Ck., 14°29.42'S 125°47.26'E, 3.v.1992; 5Pe, Mertens Falls, 13°50'S 125°43'E, 4–5.v.1992.

Non-Australian. BRUNEI, 2Pe, Kuala Belalong, Kuala Belalong Field Study Centre, 04°33'N 115°09'E, -.viii.1995.

NEW CALEDONIA: 2Pe, S. Prov., Chutes de Madeleine, 22°14'S 166°52'E, 1.ii.2003; 2L, 1Pe, Mt Mou, Road Crossing, c. 200 m. asl, 22°04'S 166°20'E, 26.i.2003.

SINGAPORE: 2L, Nee Soon swamp, site #2, 01°23'N 103°48'40"E, iii.2009 ('*NUS team'*) (TMSI).

Description. Adult male (n = 10, less for some legs). B.l. 2.9–3.9 mm, W.l. 1.4–1.8 mm.

Fl_{1-12} 396–428. Fl_{13} 573–682, A.R. 1.40–1.59.

Temporals 9–12 uniserial, some long; Clyp 14–26. Palp 2–5: 36–50, 136–208, 118–185, 159–318.

Thorax with double hump, anterior shallower than posterior. L.aps absent. Dc 8–14, Pa 2–3, Scts 3–9.

Wing. Plain. V.R. 1.01–1.12. Vein setation: R 11–22, R_1 9–17, R_{4+5} 13–22, squamals 0–5.

Legs (Fig. 1E). Apically curved spur on each mid and hind outer comb, inner comb with small, blunt spur barely extending beyond longest comb teeth. LR_1 2.0–2.2, LR_2 0.60–0.65, LR_3 0.83–0.88. BV_1 1.7–1.8, BV_2 3.2–3.5, BV_3 2.5–2.7. SV_1 1.25–1.3, SV_2 3.3–3.6, SV_3 2.46–2.5.

Hypopygium (Figs 1F, 1H). TIX bare; anal point parallel-sided, with bluntly tapered apex. SVo (Fig. 1H) ca. 50–60 µm, with 2 inner setae, 15–22 long, bases 5–12 µm apart, each arising from tubercle; 3rd very fine seta, 10 long, present in some specimens either between, or distal to strong inner setae. Mvo stem ca. 30 µm, with 20–30 split semi-taeniate and simple setae. Gcx 113–160, Gst 96–108.

Adult female (n = 1) as male, except: B.l. 2.9 mm, W.l. 1.5 mm.

Antennal ratio 0.41; apical flagellomere 110. Clyp 23. Palp 2–5: 40, 190, 165, 300.

Thorax with double scutal hump, anterior shallower than posterior. L. aps absent. Dc 11–12, Pa 3; Scts 11–12.

Wing. V.R, 1.08. R 24, R_1 22, R_{4+5} 27; 1 squamal.

Legs. LR_1 2.0, LR_2 0.57, LR_3 0.82. BV_1 1.7, BV_2 3.4, BV_3 2.6. $SV_1$1 1.3, SV_2 3.5, SV_3 2.7.

Genitalia as in Fig. 3.

Pupa (n = 10). Length 4.0–4.8 mm. Exuviae pale, with only slightly darkened apophyses.

Cephalothorax. Cephalic area smooth without tubercles, pale / hyaline frontal setae 30–40 µm. Thorax with weak scutal hump at anterior 1/3 with small scales mid-thorax alongside ecdysial line. Base of thoracic horn elongate oval, tracheal bundle densely packed, 20 x 15 µm (Fig. 4C). Prealar tubercle rounded-triangular, darkened (Fig, 4D).

Abdomen (Fig. 5A). Tergites II–VI with spinule patches laterally not reaching apophyses, and not extending to pleurae, narrower anteriorly than posteriorly; on VII and VIII spinule patches quite dense in anterior broad transverse band of spinules. Tergite II with row of 15–20 hooks extending 20–22% of tergite width. Pedes spurii B moderately developed. Pleural fringe on segments III–VIII. Posterolateral 'comb' on VIII with 10–14 teeth of relatively uniform size (Fig. 4H).

Larva (n = 2, reared). Head pale yellow with slightly darker golden-brown occipital margin, mandibles and mentum. Body length not measured. Head capsule length 450 µm, postmentum length 150 µm.

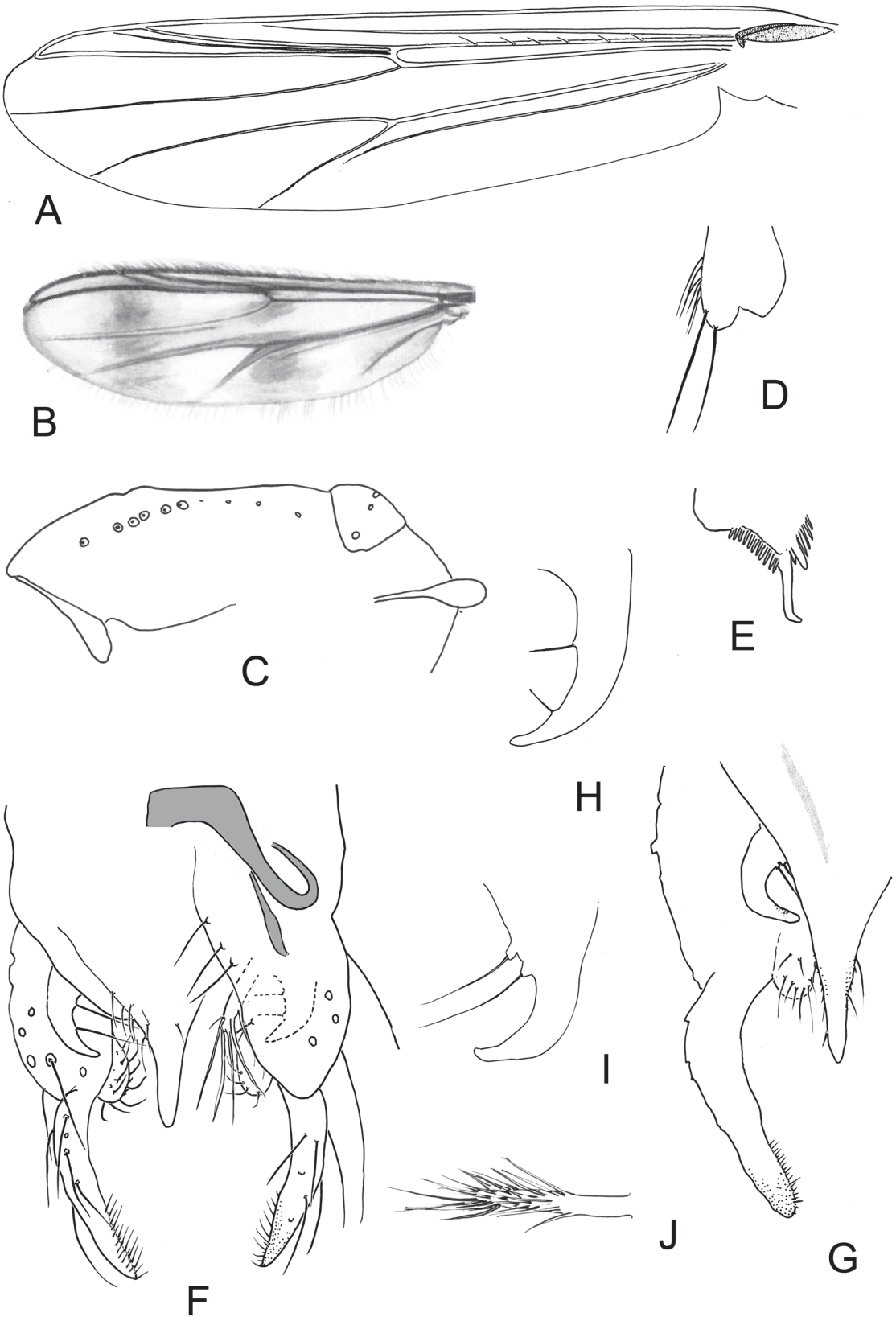

FIGURE 1. Adult *Skusella*. A, Wing, male *S. subvittata*; B, Wing, female *S. pallidipes* (from Freeman 1958); C, Lateral thorax *S. subvittata*; D, Fore tibial apex; E, Hind tibial combs and spurs *S. subvittata;* F. Hypopygium *S. subvittata* (schematic, L side of figure dorsal view, R side ventral/internal); G. Hypopygium (L side dorsal) *S. pallidipes*; H–I Superior volsella: H, *S. subvittata*; I, *S. pallidipes*; J, Median volsella *S. pallidipes*.

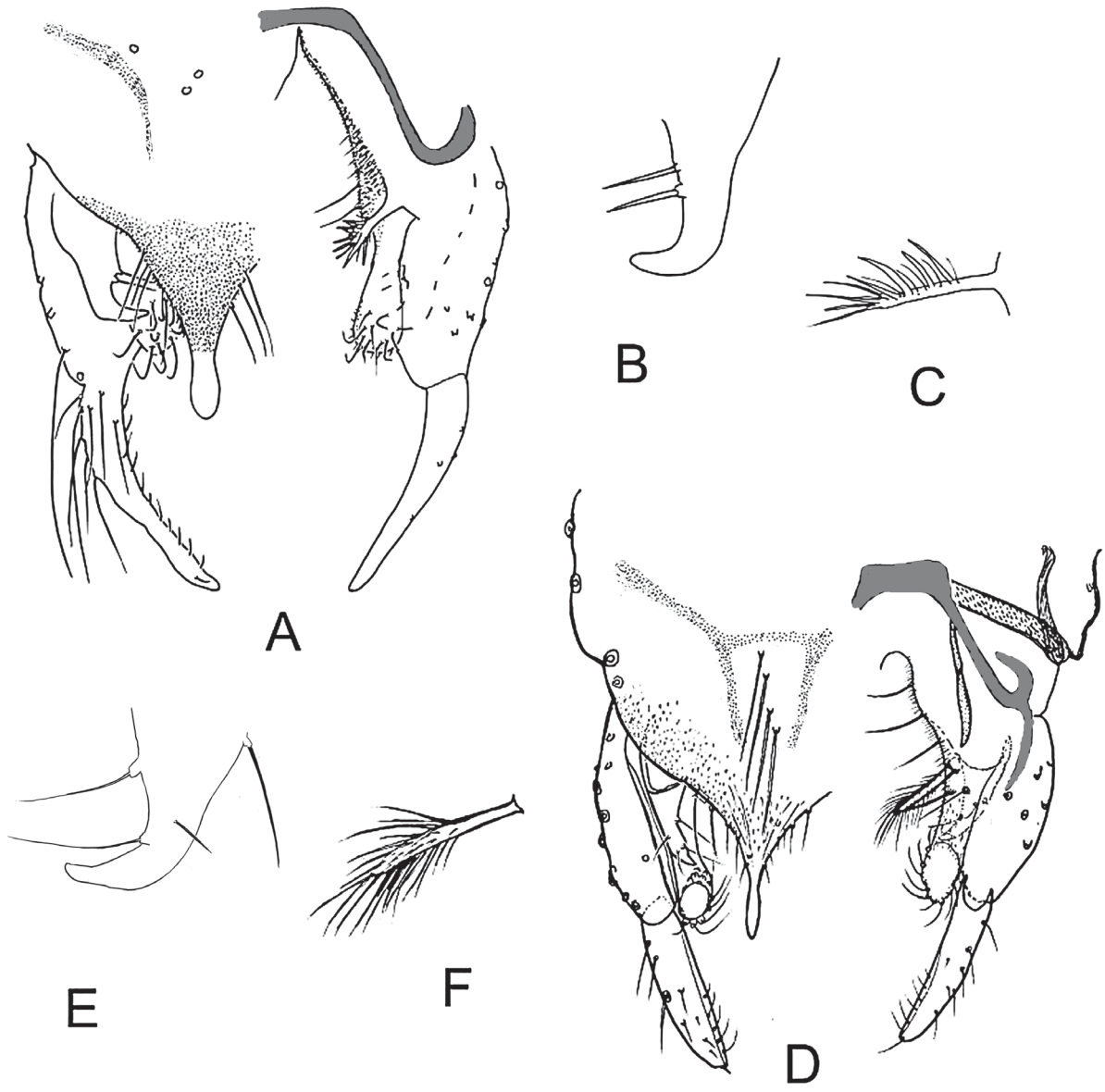

FIGURE 2. Male *Skusella*, hypopygia. A–C *S. freemani:* A. (L side dorsal, R side schematic, ventral/internal); B, Superior volsella; C, Median volsella; D–F *S. silingae* **sp. n.**: D, Hypopygium (schematic, L side dorsal, R side ventral/internal); E, Superior volsella; F, Median volsella.

Eyespots not visible. Dorsal surface of head as in Fig. 7A. Antenna (Fig. 7B) with segment lengths 87–90: 14–15: 38–42: 24–25: 5–63; AR 1.1. Lauterborn organs alternate on segment 3, 11–12 long; blade 50–62 long, extending to apex of segment 3. Labroepipharyngeal region as in Fig. 7D, premandible (Fig. 7E) 75 long, with 3 apical teeth. Mandible 110–126 long, as in Fig. 7F. Mentum (Fig. 7G) 82–90 wide; ventromental plates 108–112 wide, separated medially by 42–45.

Abdomen. Anterior parapod claws densely clustered and very pale. Posterior parapod claws golden, squat, gently curved. Procercus 20 high by 20 wide, bearing 7–8 long pale anal setae.

***Skusella pallidipes* (Kieffer, 1921)**
(Figs 1B, G, I–J; 3D; 4I, 5B)

Lauterborniella pallidipes Kieffer 1921: 52; Freeman 1958: 323.
Skusella pallidipes (Kieffer), Freeman 1961: 718, short note.

Material examined. 1♂, SUDAN [SOUTH SUDAN], Wupatong, nr Wau, 19.iii.1955 (*Reid*) BM1955-382 (NHM); 1♂ nr. Wau (*Schorch*) (NHM), 1♂, BELGIAN CONGO, Elisabethville [DR CONGO, Lubumbashi], iii.1939 (Brédo)(NHM); 1♂, 1♀, IVORY COAST, no further data (*Dejoux*) (ZSM); 1♀, NIGERIA, Anambra State, Opi Lake 1 (= Ogelube Lake), 6°45'0"N 7°29'30"E, 4–5.xi.1978, emergence trap (*Hare*)(NHM); 1Pe (putative identity), same except 28.i.–7.ii.1978.

Material mapped, not examined. Sudan [South Sudan]: Melut, Adok, Shambe; Nigeria: Katsina, Kankiya; Sierra Leone: Pepel; Gold Coast [Ghana]: Nangodi; French Cameroons [Cameroon]: Kribi; Belgian Congo [DR Congo]: Musosa; S. Rhodesia [Zimbabwe]: Salisbury [Harare].

Description. Adult male (n = 5). B.l. 6.0–6.8 mm, W.l. 2.4–2.7. Antenna: Fl_{1-12} 405–445, Fl_{13} 1115–1240, A.R. 2.75–2.92. 19–14 temporals, 17–23 clypeals. Palps (2–5): 65–75, 145–180, 190–210, 300–370. Thoracic contour double humped; L. aps 4–5; ac 0, dc 9–13, pa 2–3, Scts 6–8. Vein setal counts R 7–11, R_1 16–17, R_{4+5} 17–22, VR 1.08–1.14.

Wing patterned as in Fig. 1B (female). Vein setal counts R 16, R_1 16–17, R_{4+5} 11–16. V.R. 1.18. V.R. 1.07–1.14. Squama bare.

Legs: Fore-tibial scale large without spur, mid and hind tibial combs nearly fused, bearing 1 hooked spur. LR_1 1.65–1.80, LR_2 0.39–0.44, LR_3 0.68–0.74; BV_1 1.50–1.64, BV_2 3.30–3.50; BV_3 2.65–2.80. SV_1 1.41–1.54, SV_2 4.60–4.90, SV_3 2.88–3.00.

Hypopygium (Fig 1G, 1I–J). Bands of tergite IX very faint, nearly meeting, lacking median setae, lateral to anal point TIX has several fine long seta. Superior volsella (Fig. 1I) tapering to dorsally curved apex, with 2 long inner setae arising from large basal tubercles. Median volsella 50µm, thin stemmed, with simple setae and taeniae (Fig. IJ). Gcx 240–300, Gst 165–202; H.R. 3.05–3.86.

Adult female (n = 3, all under- or over-cleared; 1 slide label states ‘dried out’).

Body length c. 3.5–3.6 mm. Wing length 1.8–1.9 mm.

Head 9–10 temporals, 14–15 clypeals. Antenna 110–130, 65–70, 70, 60, 150, AR 0.41–0.42. Palp lengths (2–5): 40, 210–220, 220, 310–315.

Thorax. With double scutal hump, anterior larger than longer, shallower posterior. Setation: 1 L. aps, 9–10 dc, 3 pa, 3–5 scts.

Wing (Fig. 1B). Pattern similar to but fainter than male and figure (perhaps all “bleached): with two broad separate darker bands each extending full width of wing. Vein setal counts R 23–28, R_1 21–28, R_{4+5} 33–46. V.R. 1.18.

All legs damaged, all tarsomeres absent: pale, at most faintly darker at femoral-tibial junction.

Genitalia. Similar to *S. subvittata* except coxosternapodeme IX thicker, darker and more sinuous; seminal ducts more sinuous / recurved, ending very close, perhaps fused in single opening. Seminal vesicles elongate-ovoid 105–120 long, maximum width 50–60, with strong neck before recurved ducts (Fig. 3D). Notum 200 long (fused section 125–150). Gonocoxite IX small, with 3–4 long setae. Dorsomesal lobe with scattered microtrichia and mesal scales. Cerci 75 long by 45–50 wide. Tergite IX heavily setose, undivided.

Pupa (n = 1, putative). 5.6 mm long. Exuviae mid-brown with darker apophyses.

Cephalothorax. Cephalic area weakly creased with well developed cephalic tubercles but lacking frontal setae. Prominent scale-covered scutal hump at anterior 1/4. Prealar tubercle rounded. Base of thoracic horn oval, tracheal bundle densely packed, 35 x 17 µm.

Abdomen (Fig. 5B). Tergites II–VI with more extensive spinules, on II–V broad anteriorly, narrowed in midsection and posteriorly broader between apophyses; TVII–VIII with dense small spinules in anterior 1/3. Pleurae without spinules. Tergite II with row of 23 hooks extending 20% of tergite width. Vortex absent. Pleural fringe only on segment VIII. Posterolateral ‘comb’ on VIII with 11 teeth in two discrete sizes (larger lateral, smaller medial) (Fig. 4H).

Larva. Unknown/unassociated, but see Comments below and *Skusella* sp. ‘Opi’.

Comments. Material from Lake Opi, Nigeria collected by Landis Hare comprises 5 slides. Although all specimens belong to *Skusella*, the only slide (and its' label) that shows an association is a pupal exuviae with emerged female conforming to *S. freemani* Harrison (see below). A second female from an emergence trap with a clearly visible bare squama, plain legs and characteristic seminal ducts conforms to *S. pallidipes*. The presence of two species is confirmed by two differing pupal exuviae. One has a pleural fringe extending from the posterior of segment III to VIII and is associated by rearing with the adult female identified as *S. freemani*. The other, an unassociated pupal exuviae from a mass rearing, has a pleural fringe restricted to segment VIII: it is treated here as belonging to *S. pallidipes*. Larvae cannot be allocated with certainty to either species and are treated below as *Skusella* sp. 'Opi'. It is unfortunate that in the 40 years since Hare's pioneering work in West Africa there have been few further regional studies to reveal new life history associations.

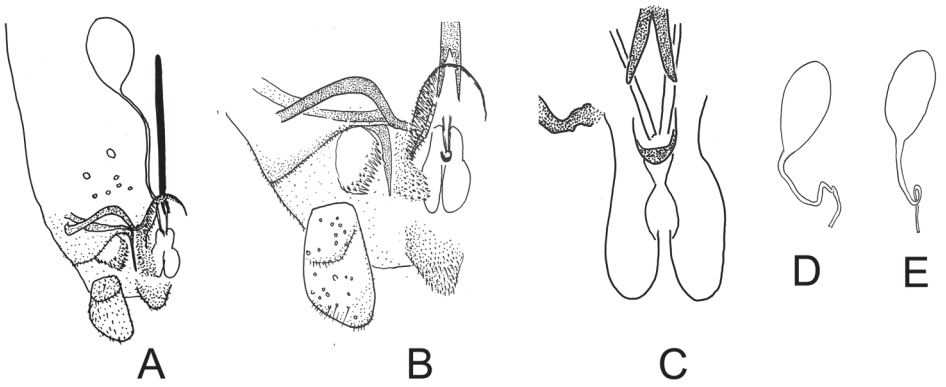

FIGURE 3. Female *Skusella*, genitalia. A–C, *S. subvittata* (reared, Wildman R.): A, Ventral (R side of body only); B, detail including apodemes and gonapophysis VIII lobes; C, detail of labia, vagina and opening of spermathecal ducts. D–E Seminal capsule and spermathecal duct: D, *S. pallidipes*; E, *S. freemani.*

***Skusella freemani* Harrison, 2002**
(Figs 2A–C, 3E, 5C)

Material examined. 1♂, Cameroon, Adamawa [Kamerun, Adamaoŭa], 20 km S. Minim, 03.iv.1979 (*Nagel & Flacke*) (ZSM). 1Pe/♀, Nigeria, Anambra State, Opi Lake 1 (= Ogelube Lake), 6°45'0"N 7°29'30"E, 10–13.xii.1978, reared (*Hare*) (NHM).

Material mapped, not examined: SOUTH AFRICA: Northern Province, Molopo Oog, Malmani Oog.

Description (data from Harrison in [ ]). **Adult male** (n = 1) total length 3.4 mm [5.5], wing length 1.9 mm [2.7].

Head. 4 temporals, 11 clypeals. Antennae missing [13 flagellomeres, A.R. 1.5]. Palp lengths (2–5): 38, 100, 100, 88 [45, 189, 201, 330].

Thorax. With single weak scutal hump. Setation: 1 L. aps, 5–6 [11] dc, 3 pa [3], 11 scts [6].

Wing basally infuscate with 2 broad transverse brown bands near contiguous in cells r_1, $r_{2+3,}$ and m_{1+2} with paler 'windows' in cells r_{4+5} and m_{3+4}. Vein setal counts R 17 [26], R_1 17 [25], R_{4+5} 13 [34]. 2–4 squamals. V.R. 1.05.

Legs yellow except distal femur and apex of tibia ('knees') on all legs brown, on forelegs distal apex of tibia also darkened. Fore and midleg tarsomeres missing. On both mid and hind tibia one comb with curved spur, the other bare.

Hypopygium (Figs. 2A–C). Tergite IX with 3 [0] anal setae. Anal point swollen, bulbous apically [rounded on holotype, more pointed on paratype]. Superior volsella strongly curved (almost hooked) medially, bearing two strong inner setae. Median volsella 30 long with simple and more taeniate setae up to 20 long (combined MV + apical taenia 50 long). Gonostylus narrowed from midpoint [moderately narrow]. Gcx 120, Gst 122, H.R. 2.8.

Adult female (n = 1) (Harrison in [ ]). Body length c. 3.5 mm [4.4]. Wing length 1.9 mm [2.6].

Head 9–10 temporals, 14 clypeals. Antenna 110, 70, 70, 60, 150; AR 0.42 [0.44]. Palp 2–5: 40, 220, 220, 310 [60, 45, 192, 207, 315].

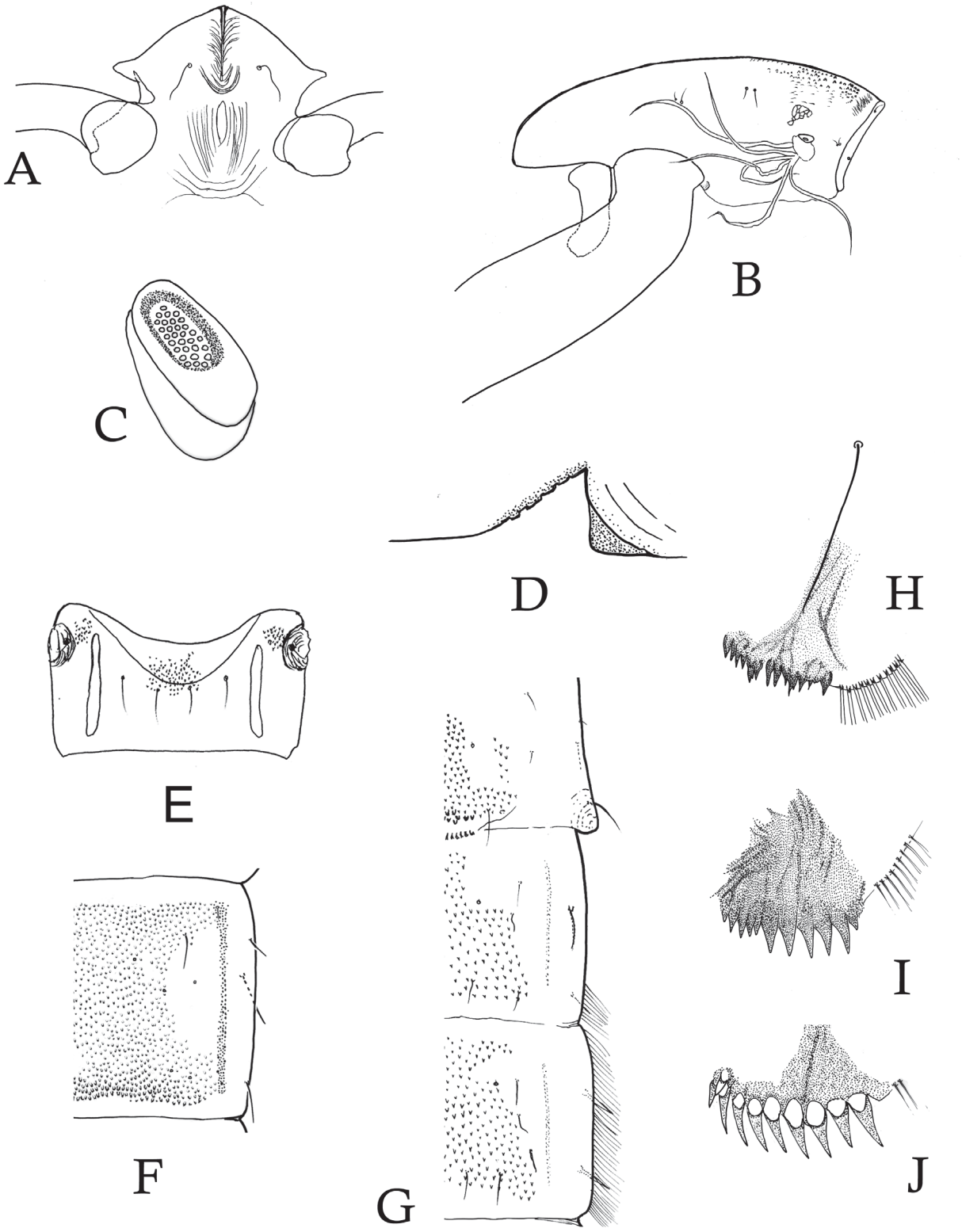

FIGURE 4. *Skusella* pupae. A, Cephalic area in *S.* sp. 'Limuling'; B, Lateral thorax, *S.* sp. 'Limuling'; C, Base of thoracic horn, *S. subvittata*; D, Prealar tubercle, *S. subvittata*; E, Sternite I, *S.* sp. 'Sanyatang'; F, Part of tergite IV, *S.* sp. 'Jianfengling'; G, Segments II–IV with pedes spurii B and pleural fringe, *S. subvittata*; H–J Segment VIII posterolateral 'combs', H, *S. subvittata*; I, *S. pallidipes*, J, *S.* sp. 'Jianfengling'.

Thorax. With double scutal hump, the anterior larger than longer, shallower posterior. Setation: 1 L.aps [1], 10 dc [15], 3 pa [3], 3 scts 10].

Wing. As in male, but fainter, with two broad separate darker bands each extending full width of wing. Vein setal counts R 23 [26], R_1 21 [27], R_{4+5} 33+ [52]. Squama damaged/missing [6].

All legs damaged but darker 'femoral-tibial junction ('knees') visible on all legs.

Genitalia as in Harrison 2002. Differences from *S. pallidipes*: seminal vesicles more ovoid, 90 long, maximum width 60, neck weak, less delimited from ducts, ducts initially directed posteriorly then making a complete loop anterior to opening (Fig. 3E, as in Harrison 2002: fig. 29).

Pupa (n = 1). Length 5.3 mm. Pale with darker mid-brown apophyses and golden 'comb'. Cephalic area with tubercles (c. 40 µm long) bearing c 30µm frontal setae, each recessed in pit. Thoracic setation and thoracic horn structure not recognisable. Prealar tubercle present.

Abdomen. Spinulation on all tergites reduced with respect to *S. subvittata*: on TII small triangular posteromedian area anterior to very short hook row (of 20 hooks, extending 20% width of tergite), spinule patches on TIII–VI narrower and sparser than in *S. subvittata*, TVII and TVIII essentially bare (Fig. 5C). Pedes spurii B well developed. Sternites I–VII bare, with anteromedian patch of fine spinules on VIII. 'Comb' on posterolateral corner of VIII with 10–11 subequal-lengthed teeth very similar to that of *S. subvittata* (Fig. 4H). Anal lobe fringe of 110 +/- uniserial taeniae.

Larva. Unknown/unassociated, but see *Skusella* sp. 'Opi' below.

Comments. The adult male from Cameroon was recognized as an undescribed species of *Skusella* by the late Dr Friedrich Reiss of the Zoologische Staatssammlung München (Reiss in litt. to Cranston, 1989). Earlier a female reared from a pupa by Landis Hare had been identified provisionally as *S. pallidipes*: here we recognise this to be *Skusella freemani* Harrison (2002). This second African species of *Skusella* was described without reference to specimens now available to us. The earlier misidentification may have been due to overclearing and/or bleaching making the wing markings very faint and the characteristic leg banding indistinct.

As recognized by Harrison (2002), *Skusella freemani* shares the patterned wing with its Afrotropical congener *S. pallidipes*. However it is differentiated by the banded femora and tibia, a setose squama, the shape and orientation of the superior volsella (curved and directed medially rather than posteriorly (Fig. 2B) and tapered gonostylus (Fig. 2A) in the male genitalia and in a looped seminal duct in the female genitalia (Fig. 3E). The Cameroon location is some 5,000 km from the type locality in Northern Province of South Africa, and the Nigerian locality even more distant. As might be expected, some variation is seen but may derive from size as South African specimens are significantly larger than those from West Africa. The conservative approach adopted here is to consider these conspecific until further evidence is available.

The associated pupa from Nigeria, described here for the first time, resembles that of *S. subvittata* and new forms from China in that the fringe extends from the posterior corner of pleura III through to apex of VIII. Differentiation includes the reduced spinulation on the tergites and, uniquely, an absence of spinules on the bare TVII and VIII.

***Skusella silingae* Tang, sp. n.**

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(Figs 2D–F, 6A)

Material examined. Holotype ♂, CHINA, Guangdong Province, Guangzhou City, Conghua District, Lyutian Town, Dongkeng Reservoir, 23°53.277'N 113°55.069'E, 9.ix.2015, light trap (*H.Q. Tang*) (EJNU). **Paratypes**, ♂, as holotype; Pe/♂ (pharate male), as holotype except 3.v.2017 (*S.L. Hu & H.Q. Tang*) (both ANIC). CHINA, 1♂, Zhejiang Province, Hangzhou City, Tianmu Mt., unnamed reservoir, 30°20.02'N 119°26.25'E, 800m asl, 27.vii.2011 (*X.L. Lin)*; 2♂, CHINA, Yunnan Province, Dehong Dai & Jingpo Autonomous Prefecture, Ruili City, Mengxiu Town, Daoba country, stream in Ruili Botanic Garden, 24°02'N 97°29'E, 31.x.2015 (*J. Liu*).

Excluded. THAILAND: 1L, Chalyaphum Prov., Amphur Chum Pae, pond, 16°35'N 102°02'E, 3.v.2004, 217 m asl, #L-660 (*Vitheepradit*); Pe, Kampaeng Phet Prov, Khlong Lan N.P., Nam Tok Klong Lan, 16°07'N 99°16'E, 8.iii.2002, #L272.

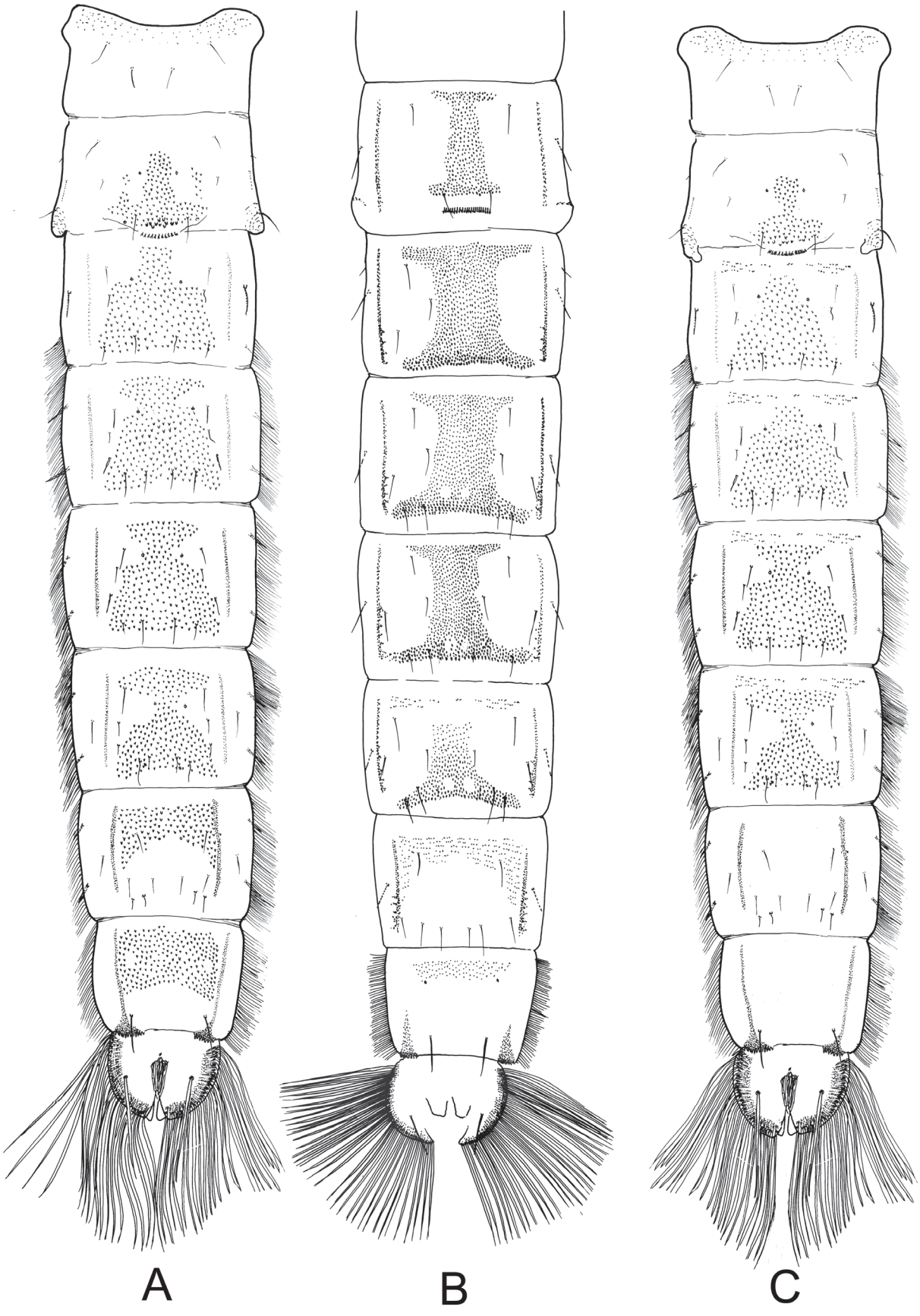

FIGURE 5. *Skusella* pupae, abdomen (dorsal). A, *S. subvittata*; B, presumptive *S. pallidipes*; C, *S. freemani*.

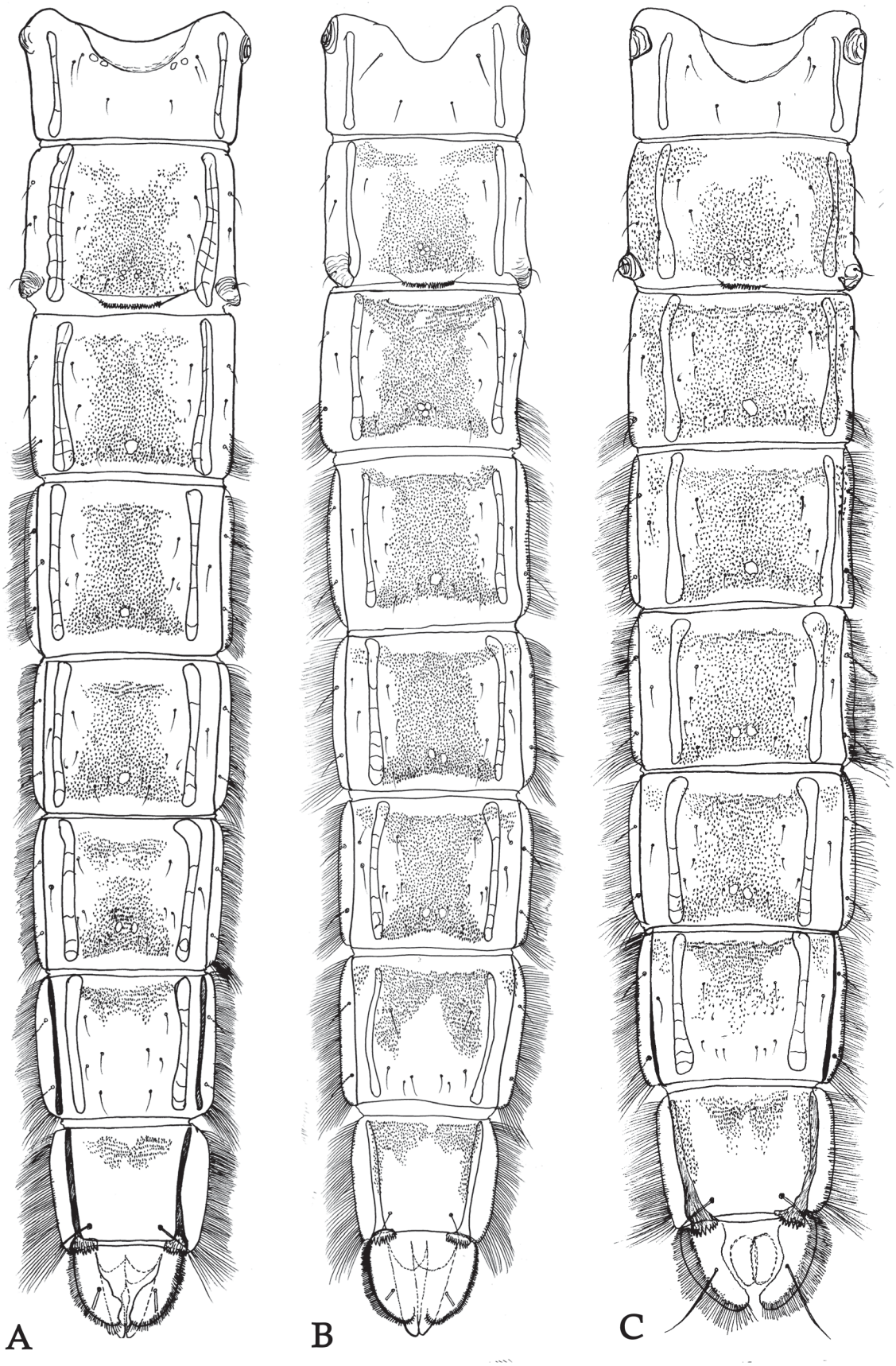

FIGURE 6. *Skusella* pupae, abdomen (dorsal). A, *S. silingae* **sp. n.**; B, *S.* sp. 'Limuling'; C, *S.* sp. 'Sanyatang'.

Description. Adult male (n = 6, 1 pharate). Similar to *S. subvittata* in colour except abdomen uniform. Legs yellow except dark brown apex of fore femur and complete fore tibia, and pale brown basal half mid and hind tibia.

B.l. 3.4–4.0 mm, W.l. 1.6–1.8 mm.

Fl_{1-12} 470–510. Fl_{13} 570–610, A.R. 1.20–1.25.

Temporals 9–12 uniserial, some long; Clyp 13–18. Palp 2–5: 30–40, 140–200, 120–170, 205–258.

Thorax with one distinct hump. L.aps 0–3. Dc 3–5 (small pits omitted), usually posterior pore still most posterior, accompanied by 2 tiny pits, Pa 2–3, Scts 6–8.

Wing. Plain. V.R. 1.10–1.14. Vein setation: R 15–21, R_1 10–19, R_{4+5} 15–24, squamals 0–1.

Legs. LR_1 2.26–2.41, LR_2 0.67–0.69, LR_3 0.85–0.95. BV_1 1.51–1.56, BV_2 3.20–3.37, BV_3 2.34–2.44. SV_1 1.18–1.21, SV_2 3.24–3.38, SV_3 2.44–2.68.

Hypopygium (Fig. 2D–F). Tergite IX with 2–4 median setae. Anal point slightly spatulate subapically. Superior volsella (Fig. 2E) ca. 50 µm, with 3–4 lateral setae, 2 inner setae widely separated (10–15 µm), arising from distinct tubercle, 1 outer seta nearly always present (at least one side). Median volsella (Fig. 2F) stem ca. 35 µm, with ca. 40 split setae.

Pupa (n = 1–2). Body length 4.95 mm. Exuviae pale grey with brown apophyses.

Cephalothorax. Cephalic tubercle low and weak. Frontal setae 50 µm, shorter than distance between setae. Thorax clearly rugose at scutal hump, otherwise smooth. Prealar tubercle seemingly absent, area damaged in dissection of pharate adult.

Abdomen (Fig. 6A). Similar to *S. subvittata*, with more extensive tergal spinulation. Pleural fringe slightly longer on IV–VII (90–100µm) than others (50–60 µm), on segment VIII slightly different to other segment, anterior ca. 75 µm, posterior ca. 150 µm. Hook row of 26–31 hooks, extending 27– 30% of segment width. Posterolateral corner of VIII ('comb') with 9–12 teeth of variable length. Anal lobe with 116–118 taeniae.

Larva. Material from Thailand may be conspecific to this species, but status will need molecular association.

Female unknown.

Etymology (Derivatio nominis). The species epithet honors the junior author's mother, Siling Hu, who helped collect the pharate material during a camping field trip.

Comments. *Skusella silingae* resembles the type species, *S. subvittata*, in the known life stages. The wing is unmarked, the anal point is more spatulate distally with a rounded apex and the superior volsella has 3–4 lateral setae, of which 1 outer seta always is present, the apex tapering more abruptly (Fig. 2E). The pupa has a pleural fringe extending from the posterior of TIII to VIII, spinulation on tergites II–IV not extending laterally beyond adhesion marks, and with at least 25 hooklets on TII, row extending more than 1/4 of segment width.

Thai material is placed here as an atypical form of *S. silingae* since the pupal hook row has 31 hooklets, occupying ca. 30% of segment width, both measures greater than in the Chinese paratype.

The type locality is a relatively clean mountain reservoir. The water temperature ranges from 13.8°C to 25.1°C, dissolved oxygen 6.0–7.2 mg/l, pH 6.7–7.8, total nitrogen 0.1–0.6 mg/l, total phosphorus 0.04–0.10 mg/l, and COD 2.4–15.2 mg/l.

Unassociated pupal types, China

Skusella sp. 'Jianfengling'

(Fig 4F, J)

Material examined. Pe (♀), slide mounted in Canada balsam, CHINA, Hainan [Jianfengling NNR, drift sample from stream at approx. 1000m elevation], 23.v.1980 (*Fittkau*) (ZSM).

Description. Pupa (n = 1). 5.2 mm long. Exuviae pale brown with darker brown abdominal apophyses.

Cephalothorax. Cephalic area smooth with minute frontal setae arising from pale area of cuticle. Thorax smooth excepting oval patch of rounded scales in mid-thorax that may be associated with weak scutal 'hump'. Base of thoracic horn elongate-oval, tracheal bundle sparsely packed, 17 x 19 µm. Without prealar tubercle.

Abdomen. Tergites II–VI with extensive spinulation, anteriorly filling area between apophyses and anteriorly extending to pleurae (Fig. 4F). Tergite II with row of 23 hooks extending 25% of tergite width. Pedes spurii B moderately developed, tapering, projecting ventrally rather than laterally (perhaps according to slide preparation).

Pleural fringe on segment VIII only. Posterolateral 'comb' on VIII with 11 teeth diminishing in size from lateral to medial (Fig. 4J).

Comments. This unreared pupal exuviae from Jianfengling, Hainan, shares uniquely with Afrotropical *S. pallidipes* a pleural fringe restricted only to segment VIII. The pupal exuviae can be distinguished principally by the tergal spinulation on III–VII extending clearly onto the pleurae (Fig. 4F). In contrast in *S. pallidipes* all pleurae lack spinules in a much more restricted spinulation pattern (Fig. 5B).

***Skusella* sp. 'Limuling'**
(Figs 4A–B, 6B)

Material examined. 5Pe, CHINA, Hainan Province, Qiongzhong County, Limuling NNR, 19°10.755' N 109°45.074' E, 11.ii.2015 (*H.Q. Tang*) (EJNU, 2 (1 slide) to ANIC); 3Pe, CHINA, Hainan Province, Lingshui Li Autonomous County, Diaoluo National Forest Park, 18°43.606'N 109°52.051'E, 26.iv.2012 (*H.Q. Tang*); 1Pe, CHINA, Hainan Province, Changjiang Li Autonomous County, Bawangling NNR, 19°06.752'N 109°11.980'E, 30.iv.2012 (*H.Q. Tang)*; 1Pe, CHINA, Hainan Province, Wanning City, 3 km away from Martyrs Memorial Park of Liulianling, 18°58.825'N 110°25.348'E, 09.ii.2015 (*H.Q. Tang*).

Description. Pupa (n = 5). Body length 5.2–5.6 mm. Exuviae pale grey with brown apophyses.

Cephalothorax. Cephalic tubercle absent. Frontal setae 40–50 µm, half the length of distance between setae (Fig. 4A). Thorax clearly rugose at scutual hump, otherwise smooth (Fig. 4B). Prealar tubercle absent.

Abdomen (Fig. 6B). Similar to *S. silingae* but with spinulae on anterior of each tergite extending more laterad including to onto anterior pleurae. Hook row of 24–27 hooks, extending 23–28% of segment width. Posterolateral corner of VIII ('comb') with 9–12 teeth of variable length. Anal lobe with 130–140 taeniae.

Comments. The pupal exuviae resemble those of *S. subvittata* and *S. silingae* but lacks a cephalic tubercle and has more extensive anterior tergal spinulation. From differs from *S.* sp. 'Sanyatang' in the spinulosity on the pleurae being restricted to small areas on segments V–VII and spinules are lacking on sternite I.

Exuviae were collected from some near pristine mountain streams and ponds.

***Skusella* sp. 'Sanyatang'**
(Figs 4E, 6C)

Material examined. 1 Pe(♀), CHINA, Guangdong Province, Guangzhou City, Conghua District, Sanyatang Hydropower Station, 23°44.468′N 113°48.216′E, 28.vii.2014 (*H.Q. Tang*)(ANIC). 1 Pe(♂), CHINA, Guangdong Province, Guangzhou City, Zengcheng, pool area of Lan stream, a dam at Shuimei Country, 23°21.318′N 113°58.070′E, 20.xii.2017 (*H.Q. Tang*) (EJNU),

Description. Pupa (n = 2). Body length 4.1–4.4 mm. Exuviae pale brown with brown abdominal apophyses.

Cephalothorax. Cephalic tubercle absent. Frontal setae 40 µm. Thorax granulate only in middle, with 8–10 rounded small beads. Prealar tubercle absent.

Abdomen (Fig. 6C). Spinulation extensive on II–VII, extending onto most pleurae lateral to adhesion marks. Hook row of 18–24 hooks, 18–22% of width of segment II. Comb with 8–12 teeth. Sternite 1 (Fig. 4E) with anteromedian and anterolateral weak spinule patches.

Comments. *Skusella* sp. 'Sanyatang' pupal exuviae generally resemble those of *S. subvittata* and *S. silingae* but differ in more extensive spinulation of tergites II to IV and with these pleurae being widely spinulose (Fig. 6C). From *S.* sp. 'Limuling' this taxon is separated by more extensive pleural spinulation and the presence of fine spinules on sternite I.

Unassociated larval types, Nigeria

***Skusella* sp. 'Opi'**
(Fig. 7C, H)

Material examined. NIGERIA, Anambra State, 2L (3rd i., 4th i), Opi Lake 'A' [=Ogelube Lake], 6°45'0"N 7°29'30"E, 1.iii.1977 (Hare) (NHM); same except 1L (2 i), Opi Lake 'D', 15.v.1980.

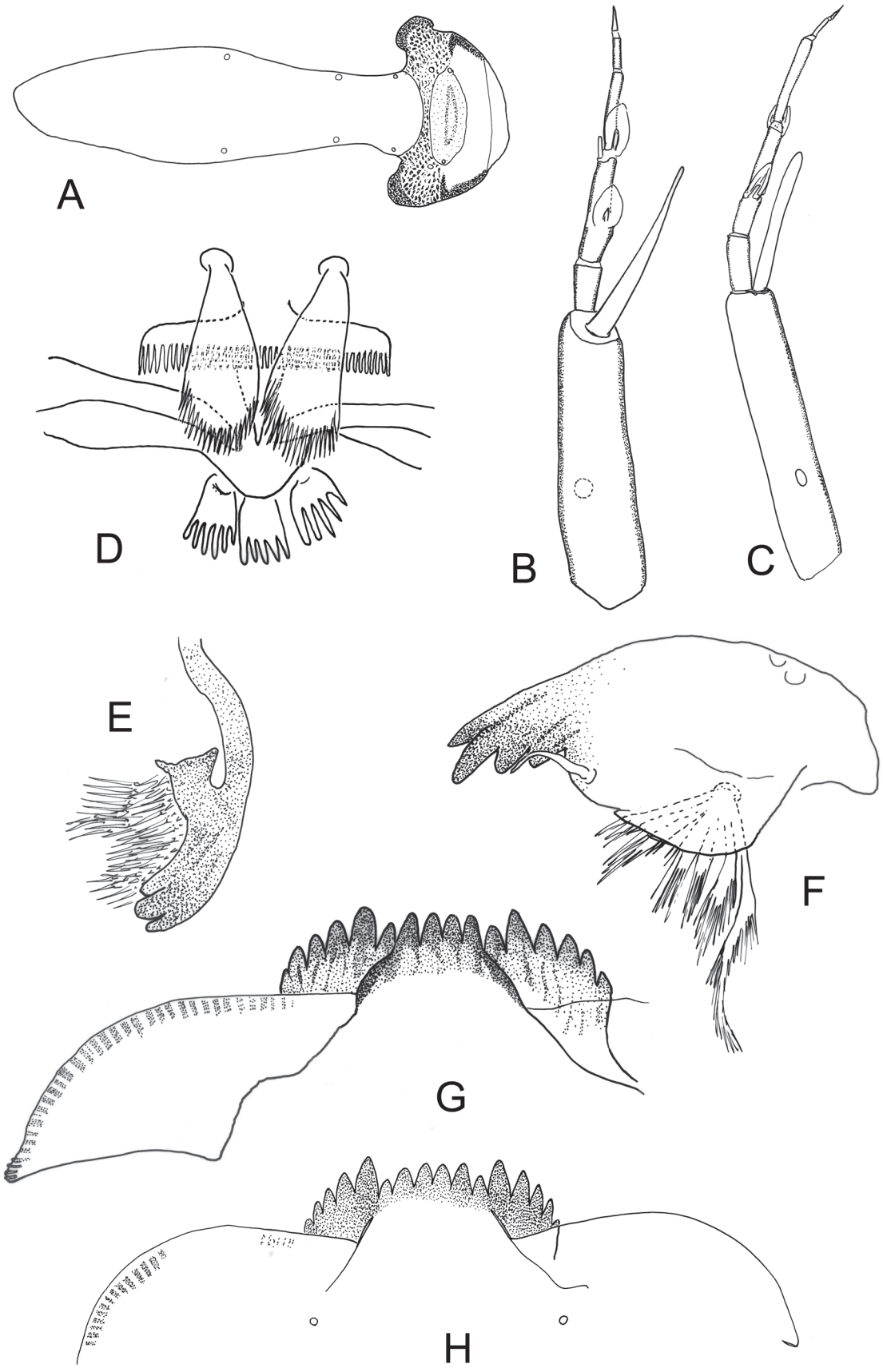

FIGURE 7. *Skusella* larvae. A, Head, frontoclypeus and parts farther anterior (dorsal); B–C, Antenna; D, Central labro-epipharyngeal region (frontal); E, Premandible; F. Mandible; G–H, Mentum. A, B, D–G, *S. subvittata*; C, H, *S.* sp. 'Opi'.

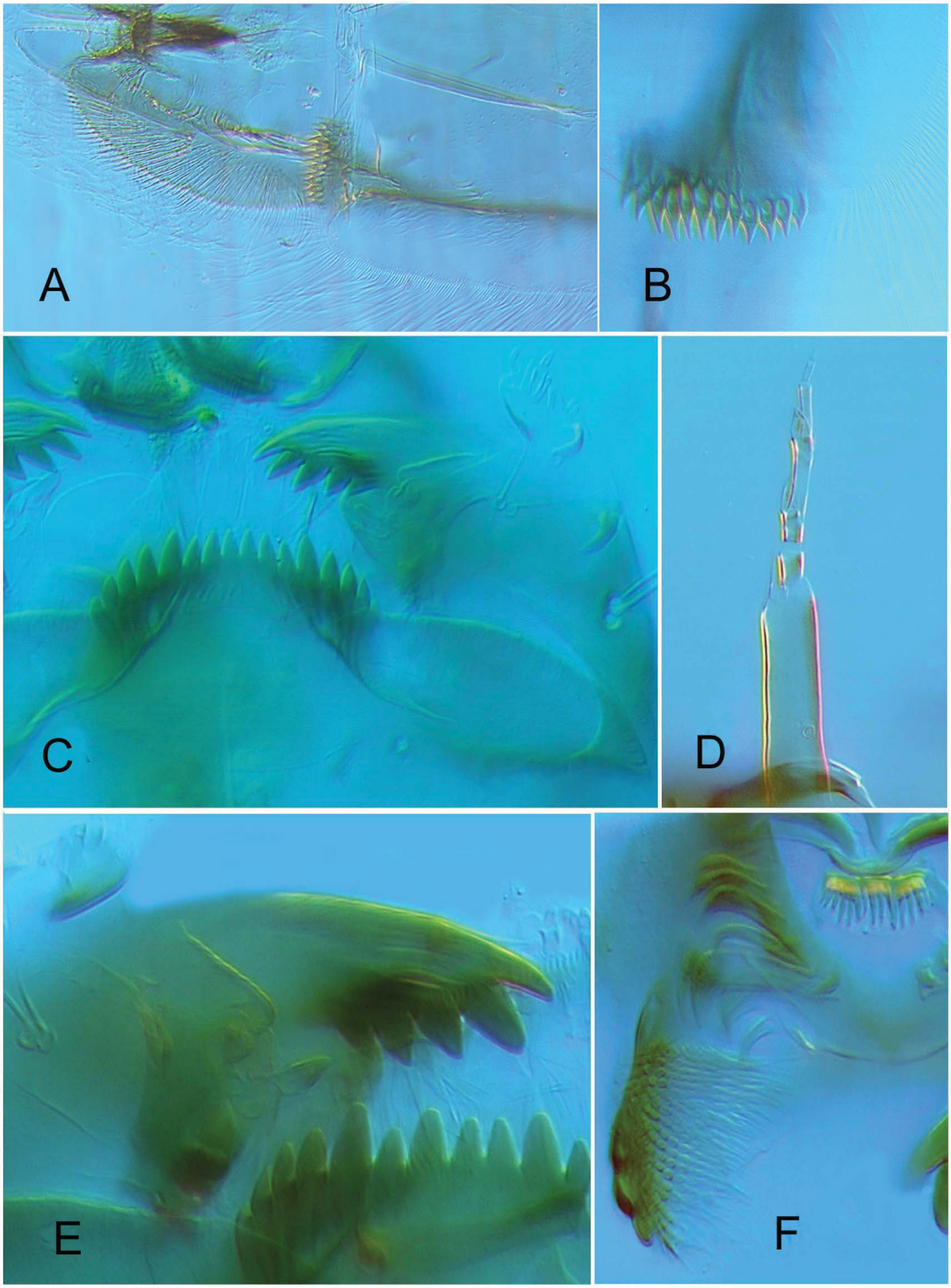

FIGURE 8. *Skusella subvittata* immature stages. A–B, Pupa: A, Segments VIII–IX; B, Segment VIII posterolateral 'comb'. C–F, Larva: C, Premandible, mandible, mentum and ventromental plates; D, Antenna; E, Mandible and part of mentum; F. Pecten epipharyngis and premandible.

Description. Larva 4i (n = 1). Head pale yellow with slightly darker golden-brown occipital margin, mandibles and mentum. Body length (extended exuviae) c. 10 mm, head capsule 500 µm, postmentum 150 µm. Antenna (Fig. 7C) segment lengths 115: 18: 45: 30: 10, 5; AR 1.06. Lauterborn organs 10 long; blade c. 60 long, extending to mid-segment 3. Labroepipharyngeal region as in *S. subvittata*, Premandible 65 long. Mandible 105. Mentum (Fig. 7H) 90 wide; ventromental plates 100 wide, separated medially by 50, VmPR 2.2.

Abdomen. Anterior parapod claws mid-yellow, simple, narrow, gently curved. Procercus pale, squat, 20 wide, 12 high, bearing 2 fine lateral seta, respectively 15 and 25 long; apically with 5 pale yellow setae 250–300 long. Posterior parapod claws pale yellow, simple, finely curved.

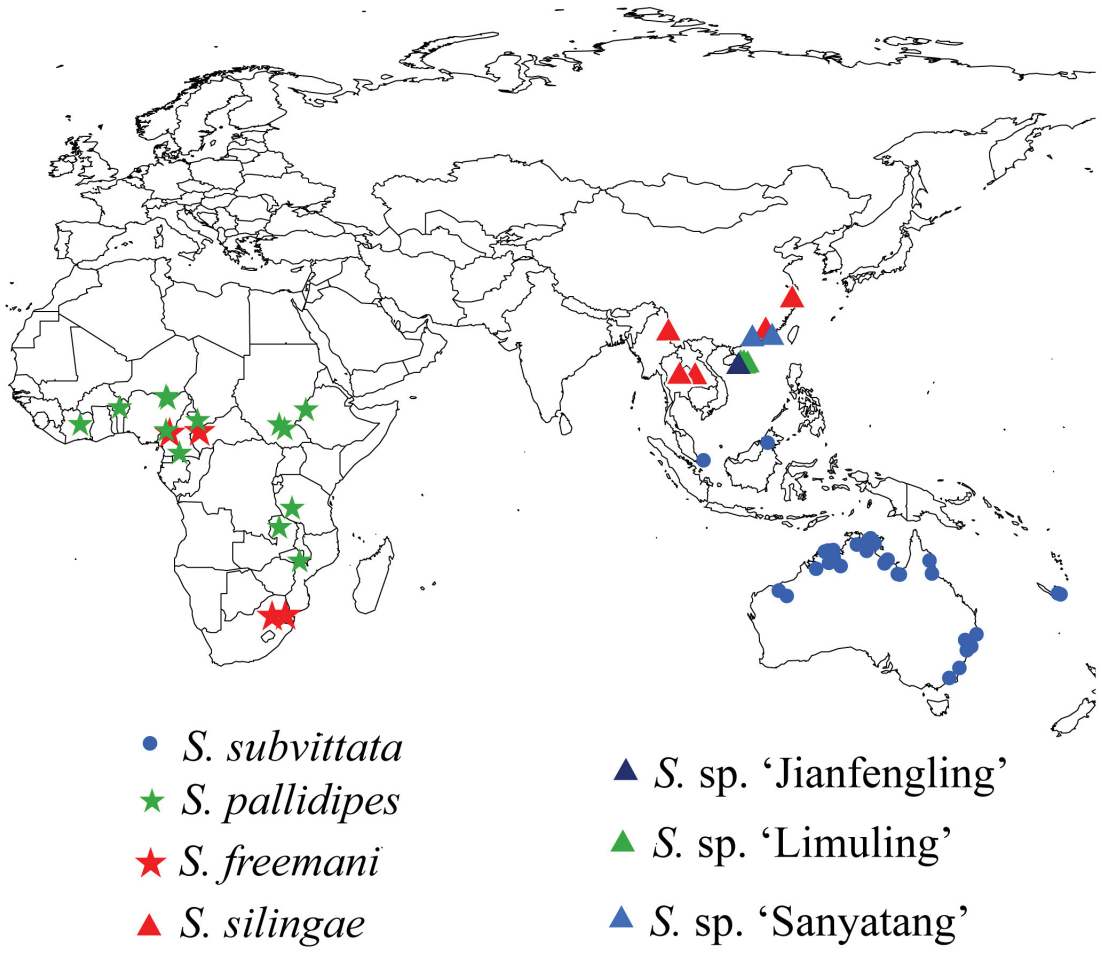

FIGURE 9. *Skusella* spp. Distribution map.

Larva 3i (n = 1) Head pale. Head capsule 250, submentum 105. Antenna 55, 8, 27, 17, 7, 4; A.R. 0.9. Premandible 65. Mandible 70. Mentum 53 wide; ventromental plates 65, separated medially by 45, VmPR 2.6.

Larva 2i (n = 1). Head pale, body red (stained ?). Body length 1.7mm. Head capsule 150, submentum 60. Antenna 30, 6, 15, 9, 4.5, 3; A.R. 0.9. Premandible 30. Mandible 70. Mentum 37 wide; ventromental plates 33, separated medially by 20, VmPR 2.6.

Comments. Material from Landis Hare from Nigeria include larval head capsules of 3rd and 4th instars. Additionally a larval exuviae under 3 coverslips on one slide is seemingly associated with the 4th instar head capsule. A second slide labelled as '2i', contains an unreared larva, of appropriate size for a second instar judging from application of Dyar's rule (% increment increase in sclerotized structure such as mandible from 3rd to 4th instar) of 1.66 between the associated 3rd and 4th instars.

No larva can be associated specifically with either *S. pallidipes* or *S. freemani* (see above). However these unallocated larvae demonstrate that larvae clearly congeneric with those of the Australian genotype (*S. subvittata)* were present at a location in West Africa where two identified species of *Skusella* occur.

Details of the larval habitat, a dilute water lake in the transition between guinea savannah and lowland moist forest in south-eastern Nigeria can be found in Hare & Carter (1984, 1987).

Discussion

Definition of *Skusella* Freeman. There seems little doubt that *Skusella* is monophlyletic, with diagnostic features in all stages (see above). Immature specimens previously included tentatively in *Skusella*, such as *Stictochironomus* cfr. *affinis* (see Appendix to this paper), are excluded. Excluded also are incompletely associated Australian taxa that had been placed informally in *Skusella* due to a pupal fringe (*e.g.* 'V12 ex WA', Cranston (1996: 284 now placed in *Paraskusella* Cranston, 2018). Of importance in this context is definition of *Paratendipes* Kieffer with regard to much morphological diversity that is formally undocumented. For example, morphology of adults includes species with and without squamal setae, with and without wing patterning and at least one species lacks the 'characteristic' spine on the anterior tibial apex (*e.g. P. inarmatus* Freeman, 1962), and one even lacks acrostichals (Hayford 1998). Too few are fully reared, and adult morphology alone seems unlikely to assist in defining the boundaries of this critical genus. In the southern hemisphere, consideration should be given to taxa putatively allocated to *Omisus* Townes, 1945 by Cranston (1996) but perhaps better associated with the New Zealand *Parvitergum* Freeman, 1959 and to *Paraborniella* Freeman, 1961. On published and unpublished life history data (P.S. Cranston *pers. obs*.) these appear distinct in their morphological and of valid generic rank, but with uncertain relationships to *Skusella*.

Distribution and ecology of the clade. The global distribution of *Skusella* is shown in Fig. 9. The genus, represented by 2 species (*S. pallidipes, S. freemani*), is widespread in Sub-Saharan Africa (the 'Afrotropical' region) with the most northerly records from South Sudan and the most southerly in eastern South Africa. The region is under-sampled in recent decades, but it may be assumed that the taxon is continent-wide in suitable habitats, both lotic and lentic, with sandy substrates.

The Australian distribution covers the warmer parts of the continent, with many records from the tropics and subtropics, some from the temperate south-west and south-east, but none from uplands and Tasmania. The genus is present in New Caledonia, but absent from the more temperate islands of New Zealand. The immature stages of *S. subvittata* occur in lotic and lentic waters, predominantly with sandy substrates, and appear to tolerate some organic pollution.

Asian records of the genus extend northwards from Australia through south-east Asia (Borneo, Singapore and Thailand) to southern China, including Hainan where 2 taxa are present. The most northerly record extends to the Mt. Tianmu, Zhejiang Province, south of the Yangtze River, which delimits the strict border between the Eastern Palaearctic region and Oriental region in China (Heiser & Schmitt 2013). With continued more intensive sampling we expect the genus to be found in the Ryukyu Archipelago, Taiwan Island and Indian sub-continental. New findings of *S. silingae* from China and Thailand, provides direct evidence for an uninterrupted distribution across an extensive range. This distribution of *Skusella* closely parallels that of the putative sister taxon *Conochironomus*, also with diversity in sub-Saharan Africa, Australia and extensive distribution recently recognised in south-east Asia (Cranston 2016). Such patterns in Chironomidae occur mostly in the tribe Chironomini, and appear to derive from a shared ecology and probably long-distance dispersal. No dated molecular phylogenies include adequate sampling to assess what, if any, role vicariance played in development of these present-day patterns.

Significance of the pupal fringe. The fringe of setae on some pupal abdominal pleurae (lateral tergites) needs discussion. In *Skusella* this fringe is expressed at least on segment VIII. Individual taeniate setae are about 1.5 microns wide with their bases evenly separated by the same distance: in this they rather closely resemble the fringe of the anal lobe of many Chironomidae. However, the pleural fringe differs from that of the anal lobe in that the setae always are uniserial, with their bases aligned tightly and linearly and never are inserted bi- or multiserially. Thus homology of the pleural fringe with the anal lobe fringe is unlikely. It could be inferred that the pleural fringe results from multiplication of conventional L setae, which may be taeniate on more posterior abdominal segment. Support would come from the absence of L setae on the pleurae of segment VIII, but is repudiated by the co-occurrence of L setae and a pleural fringe on more anterior segments.

The pupal pleural taeniate fringe of *Skusella* is unique in the subfamily Chironominae [excepting 'V12 ex WA' (Cranston 1996: 284) now placed in *Paraskusella* Cranston, 2018], allowing inference that is synapomorphic for the group. A fringe is present in other subfamilies, namely in Tanypodinae (*Djalmabatista* Fittkau, *Fittkauimyia* Karunakaran, some *Procladius* (*Holotanypus*) Skuse) and some *Tanypus* Meigen, in Prodiamesinae (*Monodiamesa bathyphila*) and in Orthocladiinae (*Epiococladius* Zavrel, *Xylotopus* Oliver). Perusal of any phylogeny of Chironomidae (*e.g.* Cranston *et al*. 2011) shows the feature must have multiple origins—for example, the fringed tanypods belong to several different tribes and are not sister taxa (Krosch *et al*. 2017) and their often multiserial and more strongly taeniate fringe differs from that of *Skusella*. Indeed, at least in *Tanypus chinensis* Wang that lacks taeniate L setae on the fringed pleurae of abdominal segments III–VII, it is possible that this kind of fringe does derive from massively replicated taeniate L setae.

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APPENDIX. Taxon excluded from *Skusella*

***Stictochironomus* cfr. *affinis* (Johannsen)**
(Fig. 10A–E)

Chironomus (*Stictochironomus*) *affinis* Johannsen, 1932: 525.
Stictochironomus affinis (Johannsen); Ali *et al*. (1987): larva, pupa, male.
'?*Skusella'*. Cranston (1996): figure, larva; Sriariyanuwath *et al*. (2015).

Material examined. AUSTRALIA: 1L, Northern Territory, Kakadu National Park, Bowerbird Billabong, 12°47'S 133°03'E, 29.v.1988 (*Cranston*)(ANIC); 2L, same except S. Alligator R., Guratba [= Coronation Hill], 13°35'S 132°36'E, 4/5.vi.1988; 1L same except Gimbat, 13°34'S 132°35'E, 24.v.1988; 1L, same except Fisher Ck., 13°33'S 132°33'E, 18/19.iv.1989.

1L., Queensland, Cape Tribulation, Oliver Ck., 16°08'37"S 145°26'21'E, 22–23.iv.1999.

CHINA: 1L, 1Pe (unassociated) Guangdong Pr., Huazhou City, Nawu Town, Ling R., Gaotiandong sect., 21°58.15′N 110°33.67′E, 22.xi.2013 (*Tang*) (ANIC).

THAILAND: several L from Chiang Rai (19°26"N 99°41'E) to Chalyaphum ((15°58"N 102°02'E) (*CMU team*) (ANIC).

Comments. A distinctive larva found in waterways prospectively impacted by uranium mining in Arnhem Land, Northern Territory, Australia was termed 'nr *Skusella'* in Cranston 1996. Larvae were unreared and no pupa or adults are associated. This larva type has been reported more recently as '?*Skusella'* from the Phong River in Khon Kaen Province (Sriariyanuwath *et al.* 2015).

Although this taxon occurs in Australian rivers where *S. subvittata* occurs, previous tentative allocation to *Skusella* surely is incorrect. The trifid (almost *Chironomus*-type) median mentum but with a distinctive demarcated ventromentum (Fig. 10A) and Lauterborn organs each respectively on the apex of antennal segments 2 and 3 (Fig. 10B) resemble the larva of *Stictochironomus affinis* as described by Ali *et al*. (1987). Their identification was based on reared adults with a patterned wing as described and illustrated for the female type by Johannsen (1932). Generic allocation for taxa such as this has been confused. In the Holarctic keys to the immature stages (Pinder & Reiss 1983, 1986) the larva keys to Chironomini genus 'B' (fig. 10.84) and the pupa to Chironomini genus 'F' (fig. 10.91), with both distinguished from *Stictochironomus*. These concepts are reconciled and now are placed in a *Stictochironomus* in a *'caffrarius*' (Kieffer) grouping.

Cranston (1996) was not alone in misunderstanding this taxon and the number of published descriptions of this taxon as new and other misidentifications may even approach those for *Polypedilum nubifer*. The reasons are similar for both: lack of complete associations from rearings and with some features in all stages not conforming fully to generic diagnoses. For example, possession of a larval antenna with alternate Lauterborn organs, although atypical, does not exclude *P. nubifer* from *Polypedilum* as evidenced from molecular studies (Cranston *et al*. 2011). However, such analyses do not exist for *Stictochironomus* and it remains uncertain if *S. caffrarius* belongs with typical *Stictochironomus*: the status may be considered open. What is clear is that it is distant from *Skusella*.

In Thailand this taxon comprised 15 % of total abundance especially in polluted sections with high phosphate and conductivity (Sriariyanuwath *et al.* 2015). Records from northern Australia include running waters lightly affected by preliminary mining activities, and at one site where feral water buffalo caused damage. The locality in Burdwan, India from which rearings derive is not described with respect to pollution.

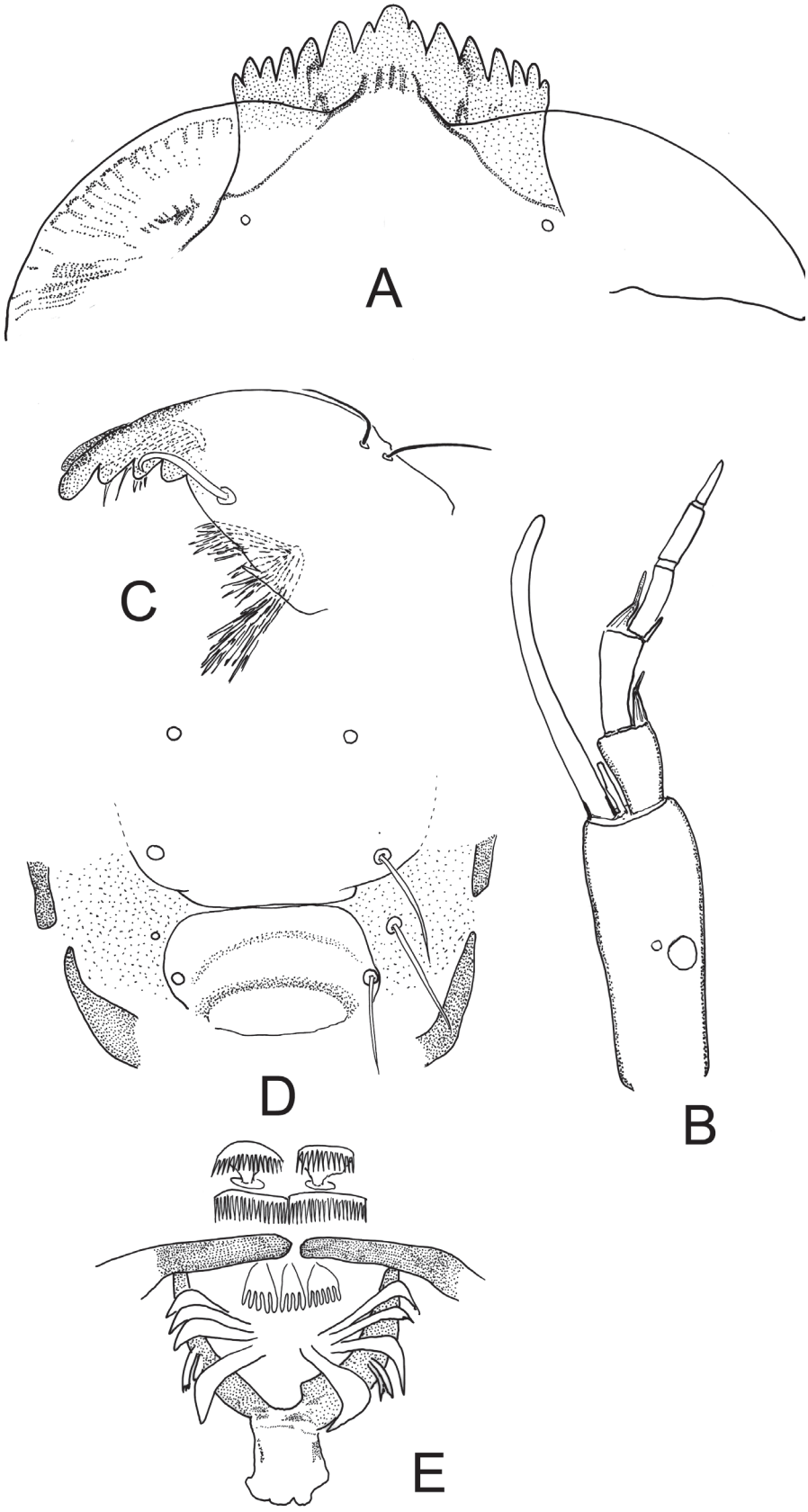

FIGURE 10. *Stictochironomus* cfr. *affinis* (Johannsen) larva. A, Mentum and ventromental plates; B, Antenna; C, Mandible; D, Head, region around anterior end of frontoclypeus (dorsal); E, Central labro-epipharyngeal region (frontal).